ISSN 0082–3449

CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 31 DECEMBER 1989

CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 31 DECEMBER 1989

PUBLISHED BY

MARINE SCIENCE INSTITUTE
THE UNIVERSITY OF TEXAS AT AUSTIN
PORT ARANSAS, TEXAS 78373-1267

FOUNDED BY E. J. LUND IN 1945

Editor: Donald E. Wohlschlag
Editorial Assistant: Rebecca Ford
Technical Editor: Ruth Grundy

CONTRIBUTIONS IN MARINE SCIENCE (Formerly *Publications of the Institute of Marine Science*) is printed at irregular intervals by The Marine Science Institute and includes papers of basic or regional importance in marine science, with emphasis on the Gulf of Mexico and surrounding areas.

Issues are distributed at a cost of $8.00 per copy (no discounts possible), or on an exchange basis.

Reprints of individual articles are distributed through the authors only.

For orders (Volumes 7 onward plus four supplements are available), further information, or exchange arrangements please write to the Librarian, Marine Science Institute, The University of Texas at Austin, Port Aransas, Texas 78373-1267. Prospective contributors should consult the Instructions to Authors included in this volume.

Copyright © 1989

INSTRUCTIONS TO AUTHORS

1. Manuscripts should be sent to The Editor, *Contributions in Marine Science*, The University of Texas at Austin, Marine Science Institute, Port Aransas, Texas 78373-1267. Manuscripts may be submitted on any aspect of marine science. Preference is given to papers relating to the Gulf of Mexico and presenting the results of original research. Papers describing new methods will also be considered. Reviews may be published but authors should consult with the editor before submitting a manuscript. Reviews will normally be considered from workers active in the field reviewed. Short notes are usually unsuitable.

   Papers will be returned to the authors for revision if the style and presentation do not conform to the journal's convention.

   All contributions are sent to outside reviewers for evaluation of scientific merit and reader interest.
2. The submission of a manuscript will be taken to imply that it has not already been published nor is being considered for publication and if accepted by *Contributions in Marine Science* that it will not be published elsewhere.
3. Manuscripts must be typewritten in English with double spacing throughout (text, literature cited, table and figure headings).
4. Page one of the manuscript should give the title in capitals, the author's name and the address(es) where the work was carried out. Footnotes may be used on the title page to indicate present addresses of authors, but should be avoided in the text. Also indicated on page one should be a short title of not more than 60 letters and spaces for use as a page heading.
5. Page two should contain an abstract. This should be concise and intelligible without the need to refer to the text.
6. The introduction should start on page three. The major headings (ABSTRACT, INTRODUCTION AND METHODS, RESULTS, DISCUSSION) should be capitalized and centered on the page. For sub-headings, capitalize the initial letter of significant words. The first sub-heading should be centered, the second shouldered and the third run-on with the text.
7. Use metric units instead of or in addition to other units. Authors should consult *Style Manual for Biological Journals*, The American Institute of Biological Sciences, Washington, D.C. for questions of general style and a list of acceptable abbreviations.
8. References in the text may be in the form "Smith (1960)" or "(Smith 1960)". When repeated references are made to papers with more than two authors, give the authors in full the first time and subsequently use the first author followed by *et al.* The full list of authors should be listed under literature cited. When reference is made to a book, the page may be indicated in the text, *e.g.*, (Smith 1960, p. 170).
9. The literature cited should be arranged alphabetically by author(s) and then chronologically, *i.e.*, Smith, A. and Abe, B. 1970, comes before Smith, A. and Brown, A. 1960. The titles of papers and the title of journals should be given in full.
10. References to books should give the editor, date, title, page, publisher's name and place of publication. The following examples illustrate the style to be followed:

    Journal:

    VAN CLEVE, R., R.Y. TING and J.C. KENT. 1966. A new device for sampling marine demersal animals for ecological studies. *Limnology and Oceanography.* 11:438–443.

    Book:

    HUTCHINSON, J. 1959. *Families of Flowering Plants.* Macmillan, N.Y. 792 pp.

    Thesis:

    HOESE, H.D. 1965. Spawning of marine fishes in the Port Aransas, Texas area as determined by the distribution of young and larvae. Ph.D. Thesis. University of Texas, Austin.

    Chapter:

    PROVASOLI, L. 1963. Organic regulation of phytoplankton fertility, pp. 165–210. In M.N. Hill (ed.) *The Sea, Vol. 2.* Interscience, N.Y.

11. Line drawings on Bristol board or good quality white paper should be drawn large enough for reduction to ½ size. They should not exceed 11 × 8½ inches.
12. Tables should be typed with IBM prestige elite 72 (12 pitch) or an equivalent, single spaced. Use a light italic (12 pitch) rather than underlining. Prepare camera ready copy.
13. Photographs should be on glossy paper. On the back of all illustrations, the name(s) of the author(s), the number of the illustration and an indication of the top edge should be given. Legends to the figures and tables should be typed on a separate sheet of paper.
14. There are no page charges but the high cost of printing may preclude the acceptance of long papers with large numbers of illustrations unless the author can make a contribution to the cost of publication.

TABLE OF CONTENTS

Instructions to Authors iii

An investigation of the heat energy budget of a coastal bay *Ned P. Smith* 1

Heavy metal content in otoliths of king mackerel (*Scomberomorus cavalla*) in relation to body length and age *John R. Grady, Allyn G. Johnson and Marion Sanders* 17

A biological and physiological characterization of the Rio Carrizal estuary, Tamaulipas, Mexico *S. C. Rabalais, W. M. Pulich, Jr., N. N. Rabalais, D. L. Felder, R. K. Tinnin and R. D. Kalke* 25

Occurrence, age and growth of two morphological types of sand seatrout (*Cynoscion arenarius*) larvae in the winter and early spring coastal waters off west Louisiana *James H. Cowan, Jr., R. F. Shaw and J. G. Ditty* 39

Redescription of larvae of the pinfish, *Lagodon rhomboides* (Linnaeus) (Pisces, Sparidae) *Glen G. Zieske* 51

Exploited and unexploited hard clam, *Mercenaria mercenaria* (L.), populations in coastal Georgia *Randal L. Walker* 61

Mortality and condition of the American oyster in Galveston Bay, Texas *Thomas M. Soniat, Lorene E. Smith and Michael S. Brody* 77

Nekton assemblages of the Calcasieu estuary *James D. Felley* 95

Aspects of the ecology of the calanoid copepod genus *Pleuromamma* in the eastern Gulf of Mexico *James L. Bennett and Thomas L. Hopkins* 119

Mortality of larval red drum (*Sciaenops ocellatus*) associated with a *Ptychodiscus brevis* red tide *Cecilia M. Riley, Scott A. Holt, G. Joan Holt, Edward J. Buskey and C. R. Arnold* 137

Occurrence of a dinoflagellate bloom associated with an influx of low salinity water at Galveston, Texas, and coincident mortalities of demersal fish and benthic invertebrates *Donald E. Harper, Jr. and George Guillen* 147

Contributions in Marine Science. (1989) Vol. 31:1–16.

AN INVESTIGATION OF THE HEAT ENERGY BUDGET OF A COASTAL BAY

Ned P. Smith

Harbor Branch Oceanographic Institution
5600 Old Dixie Highway
Fort Pierce, Florida 34946

ABSTRACT

Hourly surface weather observations from a 54-week period of time in 1973-74 are used to simulate local air-water heat energy fluxes for Corpus Christi Bay, Texas. Results show heat energy gains and losses, and the resulting simulated temperatures, varying over three distinct time scales. The annual cycle explains 82% of the variance of simulated bay temperatures. Approximately weekly variations in the storage term raise and lower water temperatures 1-2°C about the seasonal norm from May through August, and 3-4°C about the seasonal norm during the rest of the year. Diurnal variations are superimposed on both weekly and annual cycles. The mean amplitude of the diurnal cycle is 0.3°C. Seasonality appears in the magnitude and temporal variability of local heat fluxes. Evaporative cooling and solar heating are greatest during summer months. Day-to-day variations in daily mean net outgoing longwave radiation, sensible and latent heat fluxes and water-sediment conduction are significantly greater from September through April, when cold fronts move across the Texas Gulf coast. The relative importance of individual processes varies over the course of a year, but on average the energy budget of Corpus Christi Bay involves a near balance between solar heating and cooling by outgoing longwave radiation and latent heat flux.

INTRODUCTION

The physical processes responsible for energy gains and losses in any body of water are summarized by the well-known heat budget equation:

$$Qt = Qs + Qh + Qm + Qb + Qe + Qa.$$

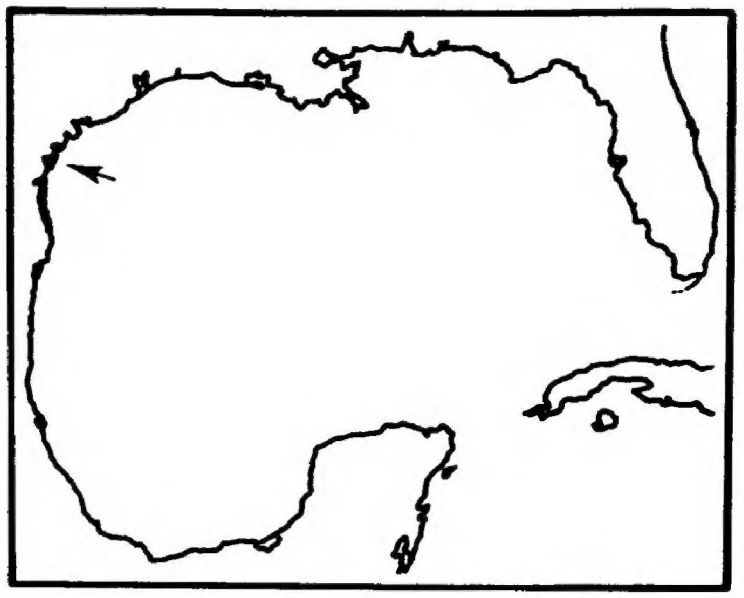
The first three terms on the right hand side represent local heating by absorbed incoming solar radiation, sensible heat fluxes and conductive heat exchanges between the water column and underlying sediments, respectively. The next two terms represent local cooling by net outgoing longwave radiation and latent heat fluxes, respectively. The final term represents the warming or cooling associated with the importation or exportation of heat by currents. The storage term, Qt, in W/m^2, can be converted to temperature to simulate warming and cooling cycles.

Heat energy fluxes affecting estuaries, and the resulting temporal variability in water temperature, typically occur over three distinct time scales. A 24-

hour cycle in water temperature occurs as a direct response to variations in incoming solar radiation. Diurnal variations in solar heating force similar variations in air temperature, humidity, cloud cover and wind speed. Thus, the diurnal periodicity is fundamental to many warming and cooling processes. Quasi-periodic warming and cooling cycles over time scales of one to two weeks result from the passage of synoptic scale weather systems through the study area. The third time scale is the annual period, stemming from the sinusoidal variation of solar heating over the course of a year. To investigate the energy budget of a coastal bay over the full range of time scales, observations of meteorological variables must be closely spaced in time, yet records must extend through a full year to quantify seasonal variations.

The Texas coastal zone is well suited for investigating meteorological forcing on all time scales, and in a variety of forms. The climate is listed as "tropical semi-arid" by Critchfield (1974), yet it is anomalous enough to be included among the problem climates (Trewartha 1981). Anticyclonic flow in the middle troposphere over the southern Great Plains in summer months suppresses convection and advects relatively dry air into Texas and the lower Mississippi Valley. Thus, mid year rainfall amounts are reduced significantly in spite of ample moisture in the lower layers of the atmosphere. Characteristically low mean annual rainfall amounts call attention to the magnitude and temporal variability of latent heat fluxes in particular, because of the effect the associated evaporative water losses have on fresh water supplied to Texas coastal bays. Climatological data (U.S. Department of Commerce 1987) indicate a multi-annual scalar average wind speed of 19.3 km/h for the International Airport in Corpus Christi, and windy conditions serve to enhance both latent and sensible heat fluxes. Frontal passages during winter months produce rapid changes in wind speed and direction, air temperature, dew point and cloud cover over time scales on the order of one to two weeks. As a result of the low latitude setting, diurnal period solar heating in summer months is intense.

Corpus Christi Bay, lying along the northwestern rim of the Gulf of Mexico (Fig. 1), is an appropriate natural laboratory for investigating local heat energy fluxes. A weather station less than 1 km from the south shore of the bay, and about 10 km from the center of the bay, records routine weather data needed to quantify air-water heat energy fluxes. A large surface area to volume ratio, combined with a relatively small mean freshwater inflow, amplifies both the magnitude and the relative importance of local processes. The bay has a surface area of 381.75 km^2, a volume of $1.316 \times 10^9 m^3$ and thus a mean depth of 3.45 m. The 29-year mean discharge for Nueces River, the primary tributary to Corpus Christi Bay, is 23.4 m^3/s (Diener 1975). Uncorrected for evaporation, this is equal to 56% of the volume of the bay per year. The accumulation of Gulf water in the bay through tidal exchanges is similarly slow. Smith (1985) has postulated a half-life for bay water of about four months due to tidal flushing. Because of the relatively slow rate at which bay water is renewed, advective heat fluxes play a secondary role to local processes in the heat budget.



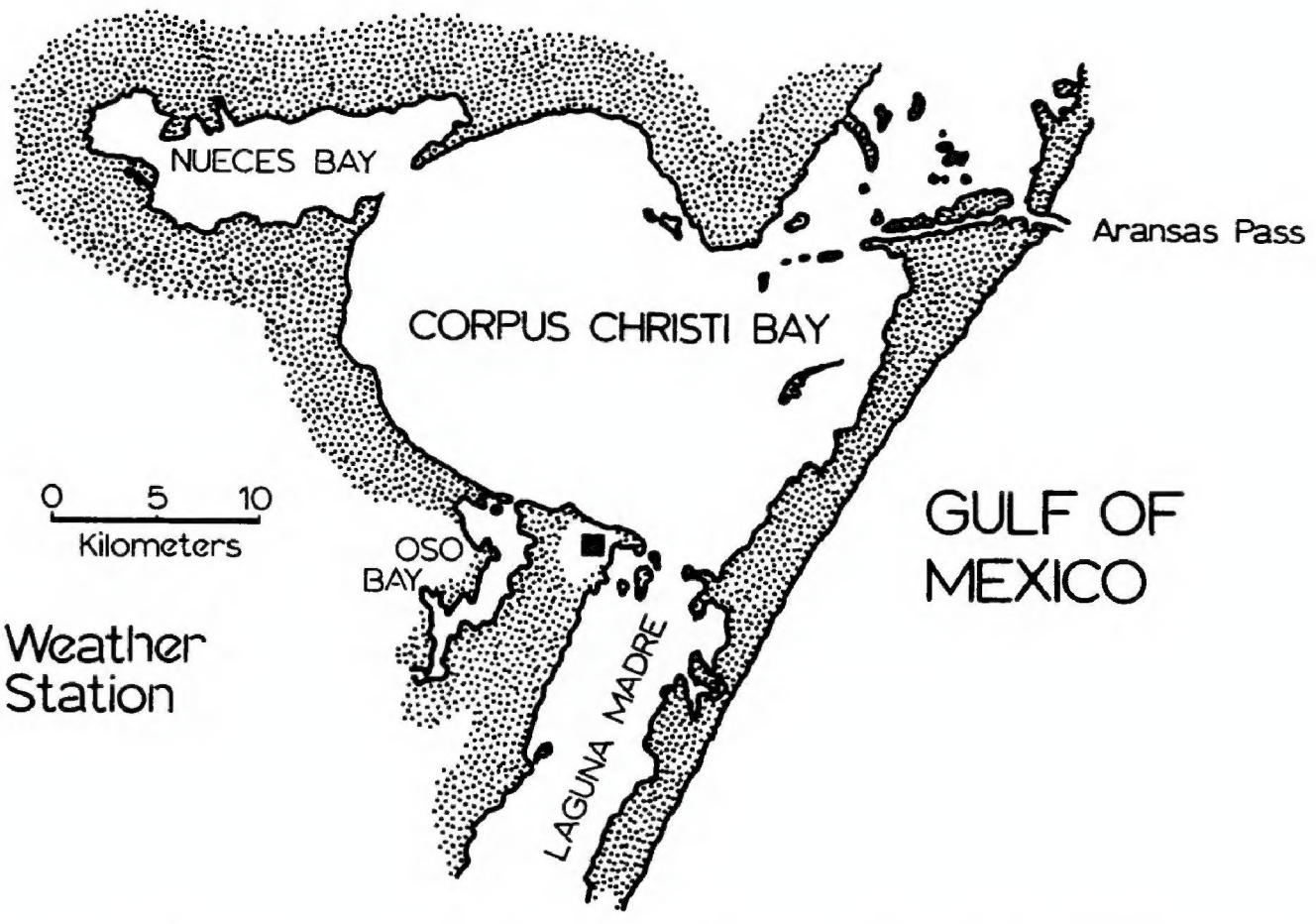


FIG. 1. Corpus Christi Bay, Texas, and the weather station on the southern shore. Insert map shows the study area in the northwestern Gulf of Mexico.

This paper presents results of a study designed to determine which physical processes control the heat budget of the bay, and the dominant time scales of each. Results indicate that the heat budget of Corpus Christi Bay is largely a balance between solar heating and cooling by evaporation and net outgoing longwave radiation. Sensible heat flux can be significant in the short term, but it is small over annual time scales. Water-sediment conduction plays a

relatively minor role throughout the year. The seasonal time scale dominates the temporal variability of water temperature; quasi-periodic, low-frequency variations in warming and cooling processes become more important in winter months, when cold fronts move through the study area. In this physical setting, the diurnal cycle is a minor perturbation superimposed on seasonal and biweekly temperature changes.

METHODS

The Data

Hourly observations were recorded at the weather station from 0000 CST, December 15, 1973, through 2300 CST, December 31, 1974. Air temperature and dew point from 2 m above a land surface were entered to the nearest degree Fahrenheit (0.6°C). Total and opaque cloud cover were estimated to the nearest tenth. Air pressure was recorded to the nearest tenth of a millibar. Wind direction was recorded to the nearest ten degrees, and wind speed was averaged visually and estimated to the nearest knot (1.9 km/hr). Climatological data (U.S. Department of Commerce 1963) from the Corpus Christi International Airport indicate that the multi-annual mean monthly wind vector has an onshore-directed cross-shelf component throughout the year; 70% of the hourly observations recorded during the present study at the weather station on the south shore of the bay were directed normal to the Texas coast (shoreward). Thus, weather data at this coastal station reflect maritime conditions for the most part.

During an 18-month period of time in 1973-75, an investigation of plankton and benthos provided monthly hydrographic data from 14 stations throughout the bay (Holland, Maciolek, Kalke, Mullins and Oppenheimer 1975). Water temperatures were recorded to the nearest 0.1°C at near-surface, mid-depth and near-bottom levels. Field data were used to calculate the mean temperature of the bay for each month, as described in the following section. The availability of field data significantly influenced the choice of 1974 as a suitable year for the energy budget study.

Methods of Analysis

The computer program developed to simulate air-water and water-sediment heat exchanges was an eclectic compilation of results of many previous studies which focused upon individual heat flux processes. Simulations were made over hourly time steps. Results of any given hour's calculation of water temperature provide the input value needed for calculating the outgoing longwave radiation, the sensible heat flux, the saturation vapor pressure needed for the latent heat flux, and the water-sediment conduction during the following hour. Simulations began on December 15 to initialize the model with observed water temperatures.

Incoming solar radiation, or insolation, was estimated using the solar constant suggested by Willson, Duncan and Geist (1980). Cloud-top reflection was quantified using values for tropical conditions and at the same latitude (Smith 1985). An atmospheric transparency of 0.75 was assumed and used both for atmospheric extinction (Miller 1981), and for entering tables of surface reflectivity (Payne 1972). Insolation calculations assumed that cloud cover was distributed uniformly from horizon to horizon. Net outgoing longwave radiation was calculated from the Stefan-Boltzmann equation, with corrections for the insulating effects of cloud cover (Reed 1976) and near-surface vapor pressure (Kondratyev 1969).

Sensible and latent heat fluxes were calculated with bulk aerodynamic formulas, as suggested by Priestley and Taylor (1972). In both expressions, wind speed recorded at the bayside weather station was increased (Hsu 1986) to approximate over-water conditions. Latent heat fluxes were determined from the specific humidity gradient (Hsu 1978), assuming that the atmosphere at the

air-water interface was saturated and equal to the temperature of the water. The gradient was defined by assuming that the weather station vapor pressure, recorded 2 m above the land surface, represented over-water conditions 10 m above the bay surface.

The flux of heat through the water-sediment interface was calculated for muddy-sand sediments, using a conductivity suggested by Geiger (1965) and a thermal diffusivity value from List (1963). Twelve, 50-cm thick sub-bottom layers were initialized with a temperature profile that assumed an exponentially-damped sinusoidal warming and cooling in the overlying medium (Sellers 1965).

In practice, the 14 hydrographic stations were sampled over a 2-3 day period. Low-frequency warming and cooling during that time prohibited a simple weighted averaging of all available temperatures to obtain mean values for the bay. A preliminary, though relatively minor correction was made to bring all bay segment temperatures together to the same point in time. Low-frequency temporal variability was estimated from a preliminary simulation which used weather data to quantify warming and cooling rates. These temperature changes were applied to individual stations to forecast or hindcast temperatures to midnight on the 15th day of each month. Time-corrected water temperatures were then combined into a single, spatially-integrated value by gridding the bay with a resolution of 1 km by 1 km (0.5 km by 0.5 km where bathymetric features were significant). Water depths at grid intersection points were estimated by interpolating linearly between nearby soundings on navigational chart C&GS 523. Volumes of surface, mid-depth and bottom layers within each segment were calculated using the Interactive Surface Modeling graphics software of Dynamic Graphics, Inc. The volume of each layer, divided by the total volume of the bay, provided the weighting factor for the associated temperature measurement. Weighted temperatures were then summed to obtain the single, bay-wide mean value needed for initializing calculations and quantifying residual fluxes not accounted for by local processes.

The advection term was not calculated directly in this study. It could only be approximated in a very crude way by the heat energy required to force a match, at monthly intervals, between bay-averaged observed temperatures and temperatures simulated by the model. This residual, however, contains all of the errors in the calculation of the five local heat energy fluxes. Thus, while it may be dominated by the advection term, it will be referred to as the residual heat flux.

RESULTS

The Seasonal Cycle

A good introduction to the results of the calculations is provided by summing hourly heat energy gains and losses, and plotting the accumulation, in kW-h/m^2, as a function of time. This form of presentation compresses both axes, and transient features and minor perturbations are suppressed. It is well suited for showing the longer period, seasonal fluctuations, however. Results are presented in Figure 2 in composite form.

Energy gains associated with incoming solar radiation are shown at the top of the plot. The curve rises relatively slowly early in the year; the mid-year accumulation is slightly faster, as a result of higher zenith angles and/or lower cloud cover amounts during daylight hours. A plot of total opaque sky cover (not shown), filtered to damp diurnal and shorter period variability, indicates that cloud cover is somewhat lower from late May to the latter part of October, but the decrease is not great. The increase in solar heating therefore seems to be primarily a result of higher zenith angles.

Cumulative energy losses due to net outgoing longwave radiation, shown in the second plot, are very nearly constant with time. The slight decrease in

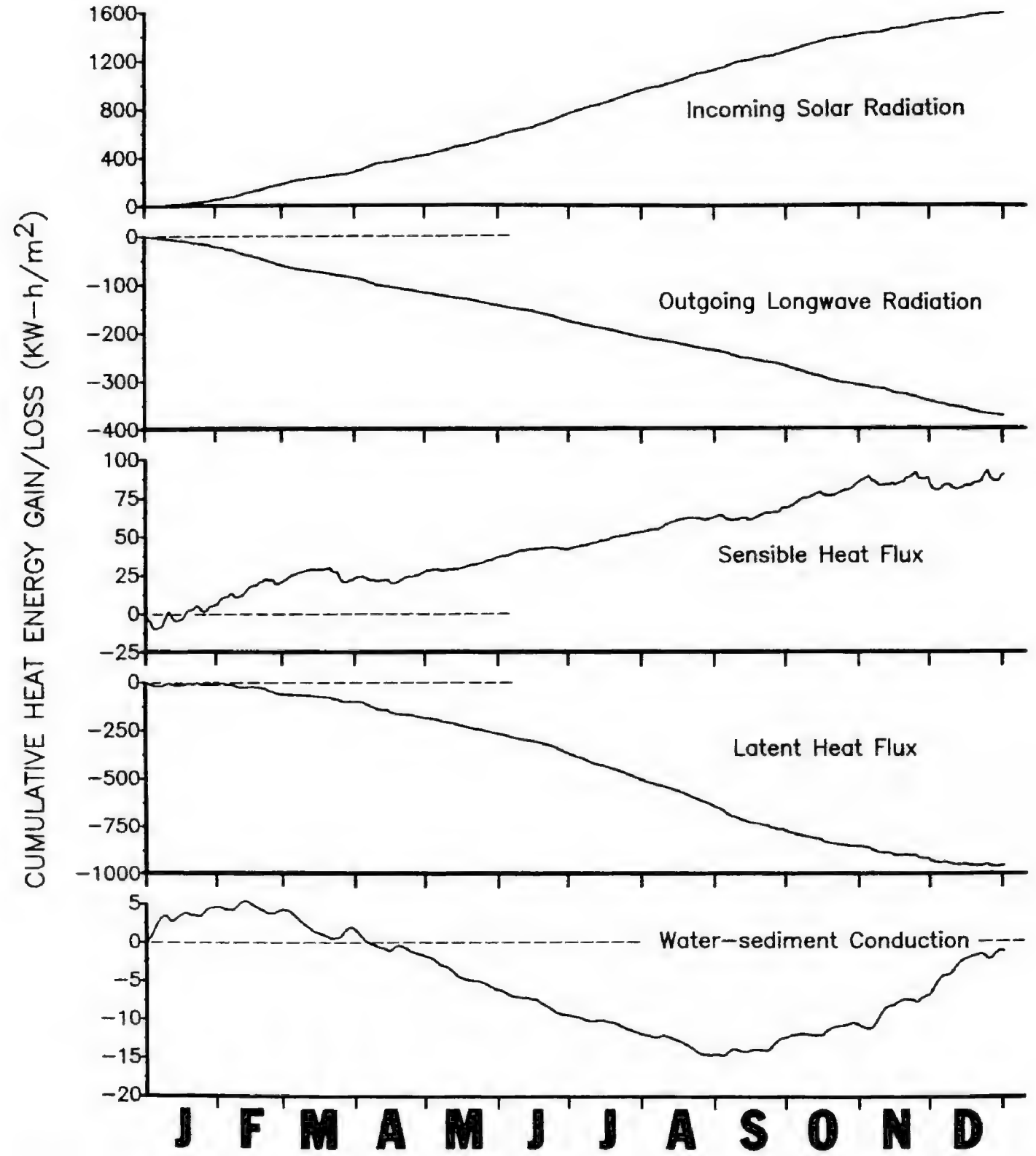


FIG. 2. Composite of cumulative heat energy gains and losses calculated for local processes, January 1 - December 31, 1974.

cloud cover noted above would, by itself, permit greater radiative energy losses, and thus increase the slope of the curve. Combined with higher water temperatures, radiative cooling in summer months should be considerably greater. However, vapor pressures from June through August averaged 26.2 mb—twice the mean value calculated for December, January and February, and 28% greater than the annual mean. Increased moisture in the lower atmosphere tends to insulate the bay, and the net radiative loss is decreased. In this case, the vapor pressure correction very nearly cancels the increase

which would occur in response to water temperature and cloud cover effects combined.

Sensible heat flux, in the third plot, is shown on an expanded scale. This process serves as a heat source on average, however transient periods of heat loss are indicated, especially early and late in the year when cold fronts bring relatively cool continental air masses to the Texas Gulf coast.

The latent heat flux exhibits a seasonality in the sense that the curve becomes steepest in mid year. Relatively slight heat energy losses are indicated early and late in the year. Evaporative cooling is a function of wind speed and the specific humidity gradient. Low-pass filtered plots of these two variables (not shown) suggest that higher midsummer evaporation is due more to an increase in the specific humidity gradient than to higher wind speeds. The specific humidity gradient exhibits a distinct seasonal variation, while seasonally averaged wind speeds vary only slightly. During June-August, over-water wind speeds averaged 24.2 km/hr—only 0.4 km/hr above the average for the year, and within 1.5 km/hr of other seasonal means.

The plot at the bottom of Figure 2 shows the heat flux into the water column through the water-sediment interface. Calculations used assumed values for sediment conductivity and thermal diffusivity. Thus, while the temporal variability indicated in the plot is probably valid, the magnitude of the fluctuations is open to question until thermal properties of bay sediments can be verified. Over the longest time scales, this process should show no net heat flux. Over shorter periods, however, a net warming or cooling may be indicated. Significant changes are expected in spring and autumn seasons, but a more subtle net warming or cooling may occur even over annual time scales, if, for example, a relatively mild winter follows a relatively intense winter, or vice versa. In this study, calculations indicate a very nearly balanced condition. The cumulative heat flux through the water-sediment interface was only -1.2 kW-h/m^2, which is 2-3 orders of magnitude smaller than any of the other terms. Equally significant is the result that the cumulative heat energy per unit area remained small throughout the year. Results therefore suggest that water-sediment conduction is the least significant term contributing to the heat budget of Corpus Christi Bay.

Table 1 summarizes the above results by providing both seasonal and annual mean values. The decision to subdivide the year into four seasons was guided by the curves presented in Figure 2, however these definitions are somewhat arbitrary. Seasonal mean insolation values show the expected summer maximum. A well-defined seasonal cycle is also apparent in the latent heat flux averages, with mid year minimum values offsetting the effects of absorbed insolation. It is noteworthy that the mean summer evaporative heat energy loss is over four times greater than that calculated for the winter season.

Little seasonal variation is apparent in either the net longwave radiation or sensible heat flux. Both the sensible heat flux and water-sediment conduction remain relatively small in magnitude throughout the year. Mid year negative values calculated for water-sediment conduction are consistent with the

significant thermal lag of sediment temperatures, as noted above. Residual heat fluxes are consistently negative, and no seasonal pattern is apparent. As noted earlier, and as discussed in the following section, it is likely that this term is influenced significantly by errors from the five local heat flux terms, even though it may be dominated by advective heat fluxes.

Small values for the storage term suggest a nearly balanced condition in winter and summer seasons. However, pronounced energy gains and losses are calculated for spring and autumn, respectively. A harmonic analysis of hourly storage values (Panofsky and Brier 1963) indicated that the amplitude of the annual cycle was only 22.9 W/m^2, and that it explained less than 1% of the variance in the time series. The annual mean calculated for the storage term is very nearly zero. Annual mean values for the five other terms indicate that the heat budget of the bay can be characterized generally as solar heating balanced by evaporative and radiative cooling.

Quasi-periodic, Low-frequency Cycles

Figure 3 uses 24-hour average energy gains and losses to highlight the low-frequency response to meteorological forcing. In this paper, the term "low-frequency" is used to refer to time scales on the order of 5-10 days. The curve for the insolation term combines light and dark conditions in the 24-hour averages. While this is not a good representation of either daytime or nighttime conditions, it is a necessary step before one can compare this term with other processes sharing the same fundamental periodicity. In this format, the seasonal variation is relatively subtle. The dominant feature of the plot is the day-to-day variability associated with changes in cloud cover as synoptic scale weather systems move through the study area. Fluctuations over these shorter time scales in summer months are about 85% of those in spring and autumn, but a seasonality in the variability of 24-hour average insolation is a minor feature.

Diurnally averaged net outgoing longwave radiative losses are shown in the second plot of the composite. There is some indication of greater day-to-day variability during months when frontal passages alternate continental and maritime air masses and produce low-frequency variations in cloud cover. Summer months show less variability, and radiative losses are more consistently at lower (less negative) levels. This demonstrates the insulating effect of water vapor in the lower layers of the atmosphere.

Low-frequency sensible heat fluxes are distinctly greater in magnitude during winter, spring and fall months, when maritime and continental air masses alternately blanket the Texas coastal zone. The relatively rapid rise and fall of air temperature, combined with slower changes in bay water temperature, reverse the sign of the air-water temperature difference over time scales on the order of a week. In summer, when both air and water temperatures are high, the sensible heat flux term decreases in both magnitude and variability. The standard deviation of the 24-hour averages during June-August is only 21% of the value calculated for December-February.

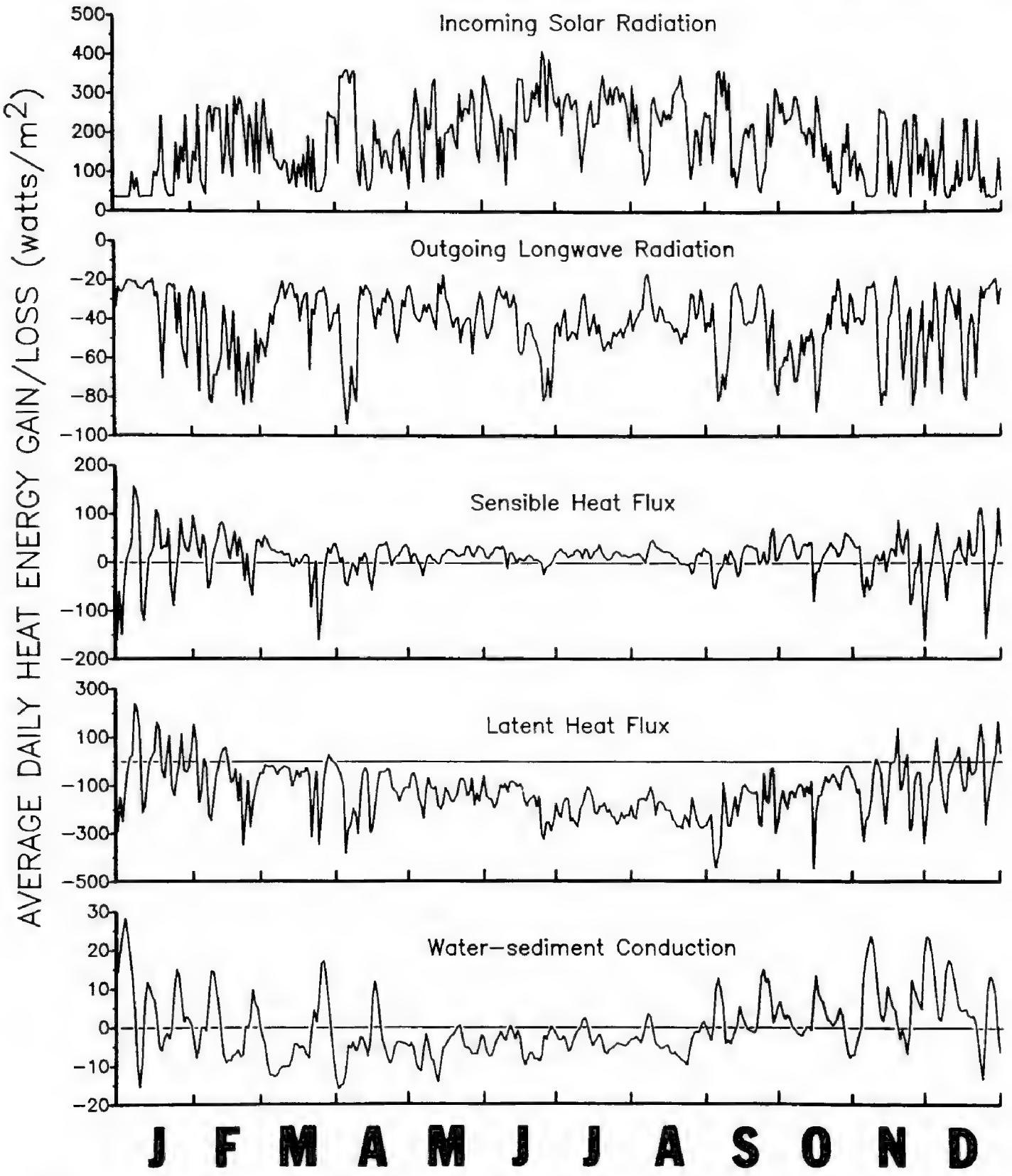


FIG. 3. Composite of 24-hour average heat energy gains and losses calculated for local processes, January 1 - December 31, 1974.

The latent heat flux also responds to alternating air masses, insofar as there is a corresponding variation in vapor pressure. The curve shows considerable variability early and again late in the year; relatively little is indicated during May-August. The standard deviation of daily mean latent heat flux values during June-August is 48% of the value calculated for December-February. In the case of evaporation, however, mid year is a time of maximum heat energy loss, if not maximum day-to-day variability. The maximum in evaporative heat energy loss occurs primarily in response to seasonal

changes in the specific humidity gradient. As noted above, seasonal variations in wind speed were minimal.

Water-sediment conduction is shown at the bottom of the plot, again on an expanded scale. The relatively high specific heat of both water and sediment suppresses high frequency fluctuations at all times of year, but a relatively large day-to-day variability appears early and late in the year—an indirect effect of frontal passages. Mid year fluxes are slightly negative, reflecting the temporal lag of sediment temperature, and thus the cooling effect of sediments on a water column which is at its annual maximum temperature.

The Diurnal Cycle

Mean diurnal cycles exhibited by the five local heat flux processes were investigated by combining the 365 values calculated for a given hour. For example, all latent heat flux values calculated for 0100 CST were grouped and averaged. This was repeated for all other hours within the diurnal cycle, and for each of the other processes. The resulting mean diurnal cycles are shown in Figure 4. The insolation term has the most exaggerated diurnal variation.

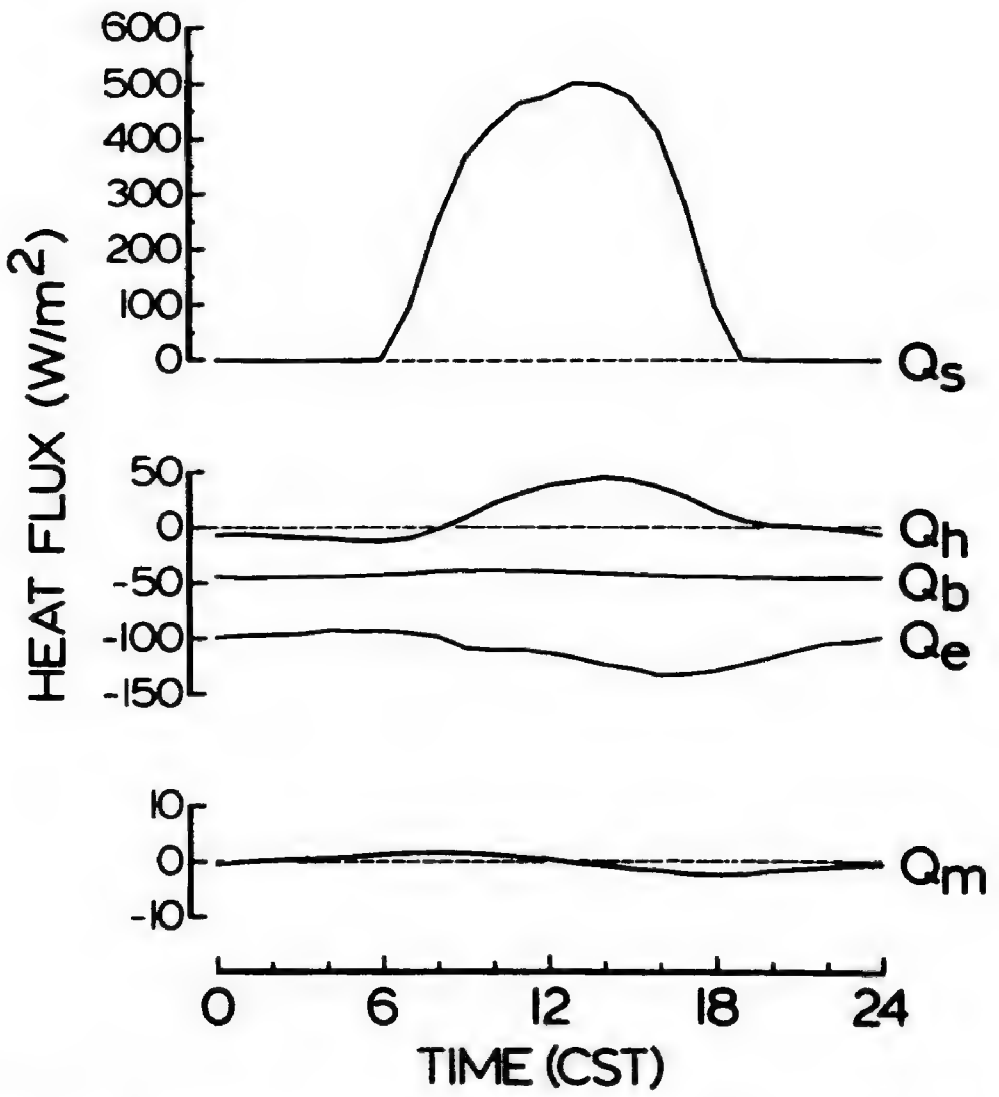


FIG. 4. Average diurnal cycle of heat energy gains and losses for local processes. Averages are calculated from the 365 24-hour periods simulated from January 1 - December 31, 1974. Symbols at right correspond to those introduced in Equation 1.

Although over the course of a year times of sunrise and sunset each vary by an hour and forty-five minutes at this latitude, essentially all of the heating by insolation occurs between 0600 and 1900 CST.

By comparison, other processes—especially water-sediment conduction and net outgoing longwave radiation—remain relatively stable throughout the course of an average day. The sensible heat flux term changes sign, becoming positive during daylight hours, because air temperatures rise and fall more than water temperatures do. The net effect is relatively small, though. The curve representing the mean latent heat flux is roughly the mirror image of the sensible heat flux curve. Values remain negative throughout an average day, and greatest heat energy losses are indicated during late afternoon hours.

Temperature Simulations

The net effect of local heat energy fluxes discussed above, plus advective gains and losses, is an increase or decrease in the storage of heat energy in the bay. This can be expressed in units of W-h/m^2, calories or, perhaps more meaningfully, in terms of the temperature of the bay—spatially averaged, as discussed in the preceding section. Figure 5 is a plot of simulated bay temperatures for 1974. Calculations were initialized with field data collected

FIG. 5. Simulated hourly water temperatures for Corpus Christi Bay, January 1 - December 31, 1974.

in mid December, 1973, although the plot begins on January 1, 1974. The plot continues through the end of the year even though calculations can be verified only through mid December, 1974.

Simulated temperatures indicate net gains and losses of heat energy occurring over three distinct time scales. The dominant time scale is the annual cycle. A harmonic analysis of simulated temperatures (Panofsky and Brier 1958) indicates an annual temperature range of 14.5°C, centered about a mean value of 21.7°C. The annual cycle explains 82% of the variance in the curve. The annual curve has a somewhat flattened crest: temperatures remain between 28-30°C from the latter part of May into early September. Superimposed on the annual cycle are quasi-periodic, low-frequency fluctuations occurring over time scales on the order of a week. This component arises in response to synoptic scale weather systems—especially cold fronts moving through the study area. In late autumn, winter and early spring months, water temperatures may increase or decrease 2-4°C about the seasonal norm. This is about twice the variability calculated for summer months.

The diurnal temperature cycle is a relatively minor perturbation superimposed on both annual and low-frequency fluctuations. Harmonic analysis of the data used to plot Figure 5 indicates that the amplitude of the diurnal variation averages 0.3°C. Harmonic analysis of each of the 365 24-hour periods provided harmonic constants (amplitudes and phase angles) of the diurnal cycle (Panofsky and Brier 1958). The time series used for this purpose was a high-pass filtered version of Figure 5. Simulated temperatures were smoothed using a low-pass Lanczos filter with a half-power point at 37 hours, and high-frequency variations were extracted by subtracting the low-frequency output of the filtering operation from the original time series. Phase angles (not shown) indicate that maximum temperatures in the diurnal cycle are tightly clustered within a two-hour interval between 1600 and 1800 CST. Amplitudes are distributed between 0.0 and 0.5°C. Figure 6 is a plot of the amplitude of the diurnal cycle over the course of the year. Seasonality is poorly defined, although there is a suggestion of somewhat higher values in mid year. Presumably, the amplitude could be related at statistically significant levels to any of several meteorological variables—notably cloud cover—but the characteristically low amplitudes found in the Corpus Christi Bay study did not encourage a closer investigation of this feature.

DISCUSSION

Results of the Corpus Christi Bay study indicate a direct relationship between the importance of air-water heat energy exchanges and the time scale over which they occur. The annual temperature range is several times that of the low-frequency temperature range; the diurnal rise and fall in water temperature is insignificant for many practical purposes. Energy budget studies tend to be site-specific, however, and in another setting, where water is shallower, the diurnal variation could assume greater prominence. Smith

(1977, 1983) has shown mean diurnal temperature ranges as high as 3-4°C in two coastal lagoons where water depths are on the order of 1 m. Presumably the annual cycle would not vary significantly as a function of water depth in estuarine studies, because the long time scales would allow water temperatures to remain in thermal equilibrium with the warming and cooling processes.

In view of the dominance of the annual variation in water temperature (Fig. 5), the small amplitude of the annual periodicity in the hourly storage values was surprising. The explanation requires a distinction between causes and effects. This result of the Corpus Christi Bay study demonstrates that the cumulative effect of even a slight variation in the storage term can be large indeed, if the time scale over which it persists is sufficiently long. In this case, because of the annual time scale, a slight imbalance that explains only 1% of the variance in the storage term results in a gradual heating and cooling that explains over 80% of the variance in the temperature plot.

The analog plots (Fig. 3) show that seasonal variability should be thought of in terms of both seasonal mean fluxes and the low-frequency variability about the mean. Day-to-day variations in the 24-hour averages of most of the processes considered are distinctly greater from late autumn through early spring. One would expect greater day-to-day variability in winter, when cold fronts move through the study area. Summer months, in contrast bring relatively quiescent weather conditions and a corresponding decrease in

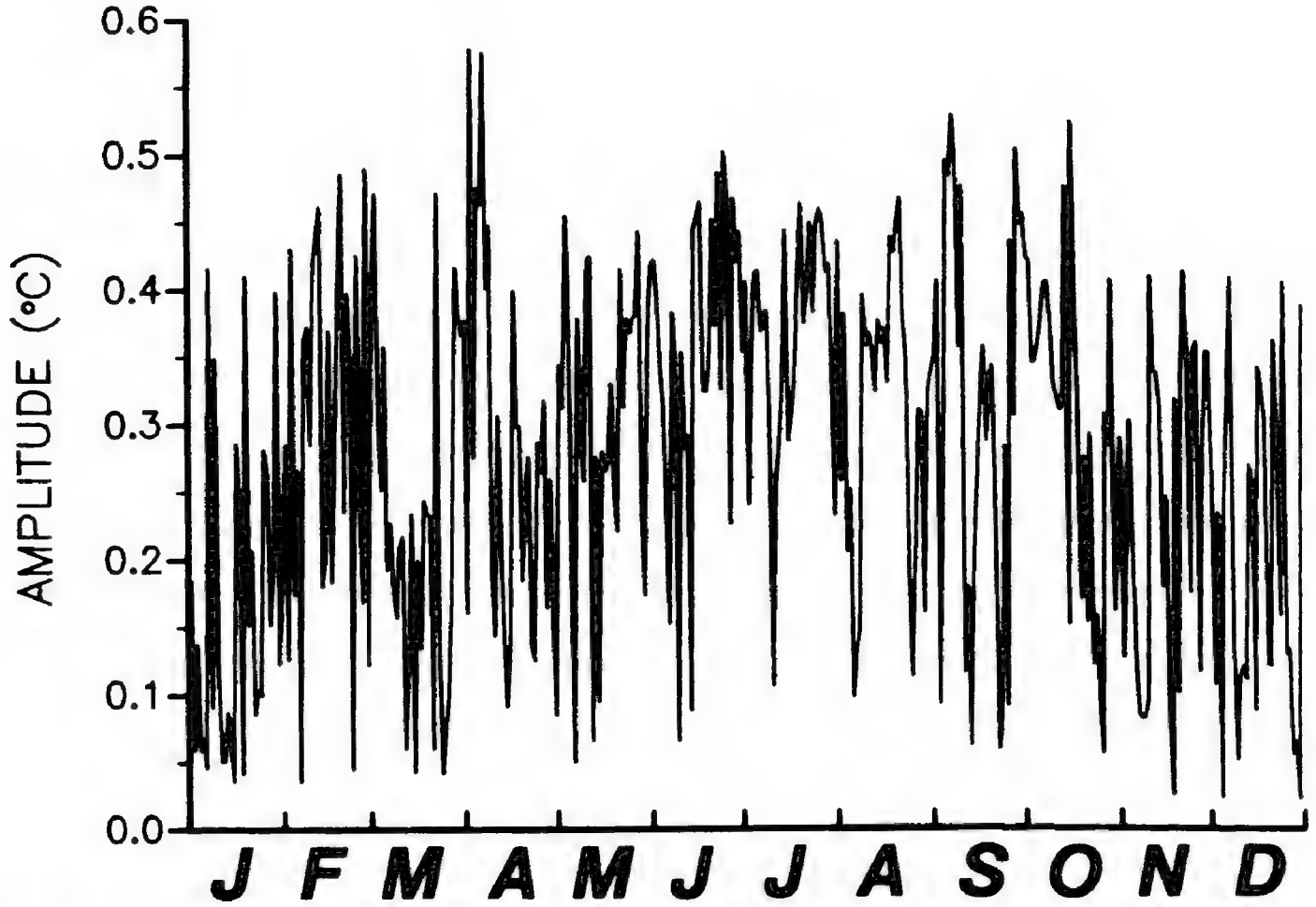


FIG. 6. Amplitudes of 24-hour period simulated water temperature variations as a function of time, January 1 - December 31, 1974.

temporal variability as relatively steady-state conditions are maintained. If processes contributing to the storage term exhibit a seasonality of this type, it follows that the same pattern should appear in simulated bay temperatures.

For Corpus Christi Bay, the relative importance of individual heat flux processes can be quantified by comparing annual and seasonal means listed in Table 1. For example, the sensible heat flux provides only 5% of the total annual heating. Conversely, the latent heat flux term contributes 57% of the total heat energy loss. The relative importance can change significantly from one season to the next, however. Latent heat energy losses, for example, increase from 30% of the total in winter to 67% of the total in summer. Similar calculations are not available for other estuaries, but one would expect considerable differences to appear. Not only would meteorological forcing vary considerably from one study site to the next, but the role of advection would be much greater in estuaries with larger tidal amplitudes and freer connection with the sea.

The importance of the latent heat flux term in controlling the heat budget of Corpus Christi Bay is accentuated by the semi-arid nature of the climate along the central Gulf coast of Texas. Evaporative water losses are more significant in view of the approximately 75 cm of annual rainfall for the region (Texas Water Development Board 1960). The annual average latent heat flux of -109 W/m^2 corresponds to an annual cumulative water loss of approximately 138 cm. Alternately, if surface evaporation is calculated using vapor pressure deficits (see Penman 1948, de Bruin 1978), a still higher value results. This latter approach was incorporated into a follow-up simulation, and an annual water loss of 265 cm resulted. Aside from the uncertainty revealed by these alternate means of estimating just one of the heat budget terms, calculations suggest that the annual water loss by evaporation constitutes a significant fraction of the effective depth of the bay—40 to 77%. Regardless of the exact

TABLE 1

Seasonal and annual heat budgets for Corpus Christi Bay, Texas. Heat energy fluxes are in W/m^2. Winter averages are calculated from simulations for December, January and February; spring represents March-May conditions; summer is defined as June-August; and autumn is September-November.

	Winter	Spring	Summer	Autumn	Annual
Incoming Solar Radiation, Qs	+118.9	+179.4	+250.6	+173.6	+181.0
Net Outgoing Longwave Radiation, Qb	-41.9	-37.8	-42.8	-47.4	-42.5
Sensible Heat Flux, Qh	+13.5	+7.1	+11.6	+8.9	+10.2
Latent Heat Flux, Qe	-39.9	-93.1	-173.8	-127.3	-108.8
Water-sediment Conduction, Qm	+4.4	-6.0	-3.8	+3.8	-0.1
Advection, Qa	-49.4	-32.2	-38.5	-38.6	-39.6
Storage, Qt	+6.0	+18.7	+3.6	-27.3	+0.3

value, in view of the relatively small amount of annual rainfall, freshwater inflow is crucial for maintaining brackish water conditions.

Another possible source of error in using routine weather data to quantify latent heat energy fluxes was the choice of 10 m for the denominator of the specific humidity gradient term. Although the moisture content of the atmosphere was sampled 2 m above the ground, that same value is probably inappropriate as the denominator of the gradient term. At a height of 2 m above the bay surface, the humidity may be significantly higher. If so, the measured, over-land value should be applied to a higher level over water. Field measurements are not available to suggest what that level might be. A value of 10 m was used in the calculations, but if this is incorrect by even 2-3 m the resulting calculations would contain errors which would be absorbed by the advection term.

The availability of monthly *in situ* data made it possible to correct the heat storage in the bay over sub-seasonal time scales. It was felt that in this way the Corpus Christi Bay study would provide some insight into at least seasonal variations in advective heat fluxes. However, calculations indicate a positive residual only during the period from August 15 to September 15. During the autumn transition season, one might expect that temperature differences between the Gulf and the bay would be greatest, because the bay would cool faster by virtue of its shallower depth. Autumn cooling does begin in late August (Fig. 5), but the fact that seasonal residuals remain negative throughout the year (Table 1) calls into question the ability of the model to single out and describe advective heat fluxes accurately by calculating them in this way. The negative residual for the year as a whole suggests that on average bay waters remain warmer than Gulf waters. This is possible, but the question cannot be resolved with the available data base. It is noteworthy in this regard that the mean bay temperature of 21.7°C simulated for 1974 is similar to the mean inner shelf temperature of 22.0°C, calculated from surface measurements made 14 km offshore during 1976-77 (Smith 1980). Also, it is important to keep in mind that advective heat fluxes can occur between Corpus Christi Bay and any or all of the other bays and lagoons to which it is connected on its landward sides (Fig. 1). Thus, the magnitude and relative importance of the advective heat fluxes remains open to question and unresolved by the Corpus Christi Bay study. It is clear, however, that an investigation of the heat energy balance for the bay is incomplete without some way to account for the residual, once local heat fluxes have been quantified and summed.

ACKNOWLEDGMENTS

Weather data used in this study were obtained form the National Climatic Center, Asheville, North Carolina. Programming assistance was provided by Paul Mikkelsen; Patrick Pitts plotted the data appearing in Figures 2, 3, 5 and 6. Special thanks to George Ward and Bill Wiseman for their objective and helpful comments as reviewers.
Harbor Branch Oceanographic Institution, Contribution No. 738

LITERATURE CITED

CRITCHFIELD, H. 1974. *General Climatology*. (Third Edition). Prentice-Hall, Inc. Englewood Cliffs, New Jersey. 446 pages.

de BRUIN, H. 1978. A simple model for shallow lake evaporation. *Journal of Applied Meteorology*. 17:1132-1134.

DIENER, R. 1975. Cooperative Gulf of Mexico estuarine inventory and study, Texas: area description. NOAA Techical Report. NMFS CIRC-393. Seattle, Washington, 129 pages.

GEIGER, R. 1965. *The Climate Near the Ground*. (Revised Edition). Harvard University Press, Cambridge, 611 pages.

HOLLAND, J., N. MACIOLEK, R. KALKE, L. MULLINS and C. OPPENHEIMER. 1975. A benthos and plankton study of the Corpus Christi, Copano and Aransas Bay systems. Final Report to the Texas Water Development Board, August 1975. University of Texas Marine Science Institute, Port Aransas.

HSU, S. 1978. Micrometeorological fluxes in estuaries. pp. 125-134. In B.J. Kjerfve, (ed) *Estuarine Transport Processes*. Belle Baruch Library in Marine Science, No. 7. University of South Carolina Press, Columbia.

_____. 1986. Correction of land-based wind data for offshore applications: a further evaluation. *Journal of Physical Oceanography*. 16:390-394.

KONDRATYEV, K. 1969. *Radiation in the Atmosphere*. Academic Press, New York, 912 pages.

LIST, R. 1963. Smithsonian Meteorological Tables. (6th Rev. Ed.) Smithsonian Miscellaneous Collections, Vol. 14, Smithsonian Institution, Washington, D.C., 527 pages.

MILLER, D. 1981. *Energy at the Surface of the Earth*. International Geophysics Series. Vol. 27, Student Edition. Academic Press, New York , 516 pages.

PANOFSKY, H. and G. BRIER. 1958. Some Applications of Statistics to Meteorology. Mineral Industries Continuing Education, Pennsylvania State University, University Park, Pennsylvania. 224 pages.

PAYNE, R. 1972. Albedo of the sea surface. *Journal of Atmospheric Science*. 29:959-970.

PENMAN, H. 1948. Natural evaporation from open water, bare soil and grass. *Royal Society of London, Proceedings, Series A*. 93:120-145.

PRIESTLEY, C. and R. TAYLOR. 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. *Monthly Weather Review*. 100:81-92.

REED, R. 1976. On estimation of net long-wave radiation from the oceans. *Journal of Geophysical Research*. 81:5793-5794.

SELLERS, W. 1965. *Physical Climatology*. University of Chicago Press, Chicago, 272 pages.

SMITH, N.P. 1977. A note of winter temperature variations in a shallow seagrass flat. *Limnology and Oceanography*. 22:1079-1082.

_____. 1980. On the hydrography of shelf waters off the central Texas Gulf coast. *Journal of Physical Oceanography*. 10:806-813.

_____. 1983. A comparison of winter and summer temperature variations in a shallow bar-built estuary. *Estuaries*. 6:2-9.

_____. 1985. The suitability of routine weather data for estimating local estuarine heat energy fluxes. *Estuaries*. 8:270-278.

TEXAS WATER DEVELOPMENT BOARD. 1960. Monthly reservoir evaporation rates for Texas, 1940-57. Austin, Texas.

TREWARTHA, G. 1981. *The Earth's Problem Climates*. University of Wisconsin Press, Madison, Wisconsin. 371 pages.

U.S. DEPARTMENT OF COMMERCE. 1963. Climatography of the United States, Climate Summary of Hourly Observations, Corpus Christi, Texas, International Airport, 1951-60. U.S. Government Printing Office, Washington, D.C.

_____. 1987. Comparative Climatic Data for the United States. National Climatic Data Center, Asheville, North Carolina.

WILLSON, R., C. DUNCAN and J. GEIST. 1980. Direct measurement of solar luminosity variation. *Science*. 207:177-179.

Contributions in Marine Science. (1989) Vol. 31:17–23.

HEAVY METAL CONTENT IN OTOLITHS OF KING MACKEREL (*SCOMBEROMORUS CAVALLA*) IN RELATION TO BODY LENGTH AND AGE

John R. Grady[1], Allyn G. Johnson[2] and Marion Sanders[3]

NOAA, NMFS, Southeast Fisheries Center
Panama City Laboratory
3500 Delwood Beach Road
Panama City, Florida 32407-7499

ABSTRACT

The maximum concentrations of heavy metals (zinc, cadmium, copper, and lead) in otoliths of king mackerel (*Scomberomorus cavalla*) were found in very young fish. The apparent decline in content of metals with age and length in king mackerel otoliths most approximated a negative power curve ($y = ax^{-b}$). The zinc content of otoliths was found to vary significantly between areas in the southeast U.S. and with the age of the fish.

INTRODUCTION

A considerable amount of information is available on the metal content in the soft tissue and skeletal structure of teleost fishes (for example, Vinogradov 1953; Hall, Zook and Meaburn 1978; Meaburn 1979), but only in recent years have the heavy metal contents in otoliths and their relationships to body length or age been investigated (Papadopoulou, Kanias and Moraitopoulou-Kassimati 1976, 1978, 1980; Macpherson and Manriquez 1977; Gauldie and Nathan 1977). Widespread interest in otoliths developed after Reibisch (1899) found that the age of fish could be approximated from the number of rings deposited in the otolith. Subsequent research on otoliths of the Teleostei has established their composition as aragonite, a polymorph of calcium carbonate, and a protein matrix. These substances are deposited in thin layers to form the growth zones that make up a chronological record of growth (Immerman 1908; Dannevig 1956; Degens, Deuser and Haedrich 1969; Pannella 1971). Investigations of the occurrence of heavy metals in otoliths are of particular interest, as otoliths remain essentially insulated concretions in the labyrinth during the life of the fish. These concretions are made of materials that are successively deposited but not removed by physiological processes (Mugiya 1964, 1974; Simkiss, 1974).

---

[1] 490 Maylin, Pasadena California 91105
[2] (Send requests to this author)
[3] NOAA, NMFS, Southeast Fisheries Center, Charleston Laboratory, P.O. Box 12607, Charleston, SC 29412

Papadopoulou *et al.* (1976) working on the zinc content of otoliths of chub mackerel (*Scomber japonicus colias*) in the age classes from zero to six years concluded that the concentration of zinc in the otoliths was a linear function of the age and body length of the fish. In a later study, Papadopoulou *et al.* (1980) found cesium, cobalt, iron, selenium and silver in otoliths of chub mackerel. They found that these metals generally decrease in concentration with the age of the fish. Macpherson and Manriquez (1977) analyzed the metal concentration in otoliths of stockfish (*Merluccius capensis*) and determined that strontium along with calcium, sodium, magnesium, and potassium appeared in constant quantity (increased with otolith weight) and that iron, copper, and vanadium only appeared in a few samples and therefore were contaminants. No attempt was made by them to relate the heavy metal concentration to the age of the fish. Gauldie and Nathan (1977) examined otoliths of tarakihi (*Cheilodactylus macropterus*) from New Zealand waters for possible contaminants from the extensive volcanic activity in the area but found only traces of zinc, copper, cadmium, nickel, and manganese. However, iron occurred in concentrations up to 7 μg per otolith, and the otolith could be placed in three groups by iron content. These groups corresponded to the three major fishing grounds of New Zealand. They found no significant increase in the iron concentration with the age of the fish. In further work on the tarakihi, Gauldie, Graynoth and Illingworth (1980) demonstrated that the iron content showed a positive regression on environmental temperature.

The objectives of our study were to determine the concentrations of copper, cadmium, zinc, and lead in otoliths of king mackerel (*Scomberomorus cavalla*) from the U.S. Atlantic and Gulf of Mexico and to determine their relation to length and age of the fish and if geographic differences could be observed. King mackerel is a migratory species important to commercial and recreational fisheries in the Gulf of Mexico and along the Atlantic seaboard of the United States (Nakamura and Bullis 1979).

METHODS

Otoliths (sagittae) were removed from 89 fresh king mackerel of known fork length (FL in mm). The fish were caught in the latter half of 1978 off Corpus Christi, Texas (15 fish), Grand Isle, Louisiana (20 fish), Panama City, Florida (33 fish), and Beaufort, North Carolina (21 fish). The otoliths were carefully cleaned and stored dry in vials.

Prior to analysis, the otoliths were immersed in glycerol (for 10-20 sec) to enhance the appearance of the growth rings for age determination. The age in years of the fish was determined by counting the number of opaque rings following the method of Johnson, Fable, Williams and Barger (1983). For metal analyses the otoliths were soaked and rinsed five or more times in hot, deionized, 18-megohm water to remove the glycerol. The otoliths were then weighed, placed with 1 ml of concentrated nitric acid in acid cleaned cylinders and allowed to dissolve for 16 h at room temperature. Nine milliliters of water were added to bring the volume of the solution to 10 ml. The zinc concentration of the otolith was determined by flame atomic absorption spectrophotometry (Emmel, Stoer and Stux 1977) using an Instrumentation Laboratory Spectrophotometer, Model No. 751[4]. The cadmium, copper, and lead concentration of the otoliths were determined by the following procedure:

[4] References to trade names do not constitute endorsement by the National Marine Fisheries Service, NOAA

1) an aliquot of the dissolved otolith was pipetted into acid treated digestion tubes;
2) one milliliter of a digestion acid mixture ($HClO_4$, HNO_3, H_2SO_4 in the ratio of 24:24:1) was added to each tube and heated to near dryness;
3) five milliliters of 1.0 M sodium acetate - 0.2 M sodium chloride buffer were added;
4) the concentrations of the metals were determined by anodic stripping voltammetry[5].

Detection limits for zinc, cadmium, copper, and lead were 1.0, 0.01, 0.05 and 0.05 μg/g, respectively, based on an otolith of 0.05 g weight. The glycerol (a single batch of No. G-7757 Sigma Chemical Company) was analyzed by the same techniques as the otoliths and found to be free of heavy metals.

RESULTS AND DISCUSSION

Obtaining representative samples of all ages and sizes of fish from various locations was difficult for king mackerel because this species is highly migratory and different fishing gear types were used, which select different sizes of fish, in different areas. Trent, Williams, Taylor, Saloman and Manooch (1983) reported on the high level of geographic variation of king mackerel sizes in the southeastern U.S.

The relationship between years (X) and fork length (Y as millimeters) can be described by the equation $Y = 598.57 + 63.0914X$ with a correlation coefficient (r) equal to + 0.9770 for the fish used in this study.

The heavy metal content in king mackerel otoliths varied between location and age (Table 1). Heavy metal content in king mackerel otoliths were generally highest in the first two years (fish less than 835 mm FL) (Table 1). The greatest concentration of zinc (49.7 μg/g) and copper (41.4 μg/g) in an otolith occurred in fish of age 0+ (fish less than 500 mm FL). The greatest concentrations of lead (15.1 μg/g and cadmium (9.38 μg/g) were found in fish of age 1+.

Examination of the data (Table 1) using multifactor ANOVA (Anonymous 1986) comparing location, age, and metal content indicated that only zinc content varied significantly ($P < 0.05$) between location and age ($P = 0.0261$ and $P = 0.0003$). We thus consider that while there appears to be relationships between metal contents and age, additional sampling is needed to confirm these observations.

The range of zinc concentration in otoliths of king mackerel (below detection limit to 49.7 μg/g) was noticeably lower than in those of chub mackerel 7 to 70 μg/g) (Papadopoulou *et al.* 1976). Papadopoulou *et al.* (1976) stated that the zinc concentration of otoliths was a negative linear function of age and growth of chub mackerel. They pointed out that the zinc concentration in the young and small fish under three years, was double that in otoliths of mature fish. In king mackerel, however, the zinc concentration of the otoliths was not linearly related to age and length. However, the relationship between age and growth and otolith zinc content was not well represented by either linear or negative power curve equations ($Y = 3.96 - 0.003X$, $r = -.57$ and $Y = 168.8X^{-.43}$, $r = -.59$).

A negative power curve ($y = ax^{-b}$) was found to approximate the apparent decline of the metal concentrations in the otoliths with growth in king

[5] Environmental Science Associates, unpublished procedure.

TABLE 1

Mean total weight and metal content of king mackerel otoliths by location and age.

Location	FL (mm) X	Age (yrs)	No. of fish	Otolith Weight (g) X	Otolith Weight (g) SD	Metal Content (micro-grams) Zinc X	Zinc SD	Copper X	Copper SD	Cadmium X	Cadmium SD	Lead X	Lead SD
Texas	632.5	1	2	0.02	0.01	0.38	0.04	0.13	0.10	0.08	0.11	0.13	0.13
Texas	763.3	2	3	0.03	0.01	0.49	0.32	0.11	0.10	0.01	X[1]	0.08	0.04
Texas	780.7	3	4	0.03	X	0.56	0.15	0.25	0.34	X	0.01	0.03	0.03
Texas	----	5	1	0.06	-[2]	0.62	-	0.02	-	ND[3]	-	0.01	-
Texas	976.3	6	4	0.06	X	0.87	1.00	0.06	0.02	ND	-	0.01	0.01
Texas	935.0	8	1	0.06	-	0.75	-	0.06	-	ND	-	ND	-
Louisiana	910.0	2	1	0.04	-	0.49	-	0.03	-	ND	-	ND	-
Louisiana	994.8	4	2	0.06	X	0.50	0.42	0.14	0.15	ND	-	0.01	X
Louisiana	1,028.0	5	4	0.06	X	0.62	0.01	0.02	X	ND	-	0.01	X
Louisiana	1,111.5	6	3	0.06	X	0.65	0.27	0.08	0.08	ND	-	ND	-
Louisiana	1,173.7	7	3	0.08	0.01	0.73	0.10	0.10	0.14	ND	-	0.02	0.03
Louisiana	1,070.0	9	1	0.08	-	0.70	-	0.03	-	ND	-	ND	-
Louisiana	1,399.0	10	1	0.11	-	0.85	-	0.10	-	ND	-	ND	-
Louisiana	1,350.5	12	3	0.11	X	1.74	1.46	0.09	0.04	ND	-	ND	-
Louisiana	1,316.0	13	1	0.11	-	0.38	-	0.03	-	X	-	ND	-
Florida	472.8	0	8	0.01	X	0.09	0.10	0.12	0.15	X	X	0.02	0.02
Florida	581.3	1	11	0.02	0.01	0.22	0.26	0.14	0.13	X	0.01	0.06	0.07
Florida	745.8	2	4	0.03	X	0.11	0.12	0.09	0.14	X	X	0.01	0.01
Florida	853.8	3	5	0.04	X	0.16	0.10	0.13	0.14	X	X	0.12	0.02
Florida	807.0	4	2	0.04	X	ND	-	0.04	X	ND	-	ND	-
Florida	918.0	5	2	0.05	0.01	0.11	0.06	0.01	0.01	-	-	0.02	0.03
Florida	996.0	6	1	0.05	-	0.33	-	0.05	-	X	-	0.01	-
Florida	1,080.0	8	1	0.06	-	0.75	-	0.06	-	ND	-	ND	-
North Carolina	704.5	1	4	0.02	X	0.35	0.22	0.05	0.01	X	X	0.02	0.01
North Carolina	741.3	2	4	0.03	X	0.27	0.13	0.19	0.05	X	X	X	X
North Carolina	810.8	3	4	0.03	X	0.49	0.35	0.04	0.04	ND	-	X	X
North Carolina	-----	4	2	0.06	X	0.50	0.30	0.15	0.10	ND	-	0.01	0.01
North Carolina	901.3	6	4	0.04	X	0.78	0.13	0.05	0.03	X	X	X	0.01
North Carolina	1,073.5	9	2	0.06	X	0.47	0.26	0.06	0.05	ND	-	ND	-
North Carolina	1,165.0	12	1	0.08	-	0.51	-	0.09	-	ND	-	ND	-

[1] X = Value less than .005
[2] - = No data
[3] ND = Not detectable

mackerel (Fig. 1). The maximum concentrations of all metals in the otoliths were found in the smaller fish.

The major accumulation of metals occur in the very early stages in the life of fish. Organic matter is also principally concentrated in the center of the otolith (Dannevig 1956). Gauldie and Nathan (1977) postulate, from their work on the tarakihi, that the metal concentration of the otoliths may be largely concentrated in the nucleus. Daily growth increments in pike (*Esox mordax*) observed by Brothers, Mathews and Lasker (1976) begins just after the absorption of the yolk-sac. These increments provide the mechanism for the permanent deposition of the metals in the nucleus.

Uptake of any metals in later years is thought to be concealed by the addition of the growth increments of protein and aragonite crystals; however, substantial annual variations appear possible if the metals are available in the environment for uptake. Large variations of metal uptake in various tissues of fish appear to be related to environmental differences in the various fishing grounds (Cross, Hardy, Jones and Barber 1973).

The usefulness of metal content of otoliths as an indicator of age and origin of fish is suggested by our results from this king mackerel study. However a more sensitive procedure such as x-ray fluorescence spectrometry and the

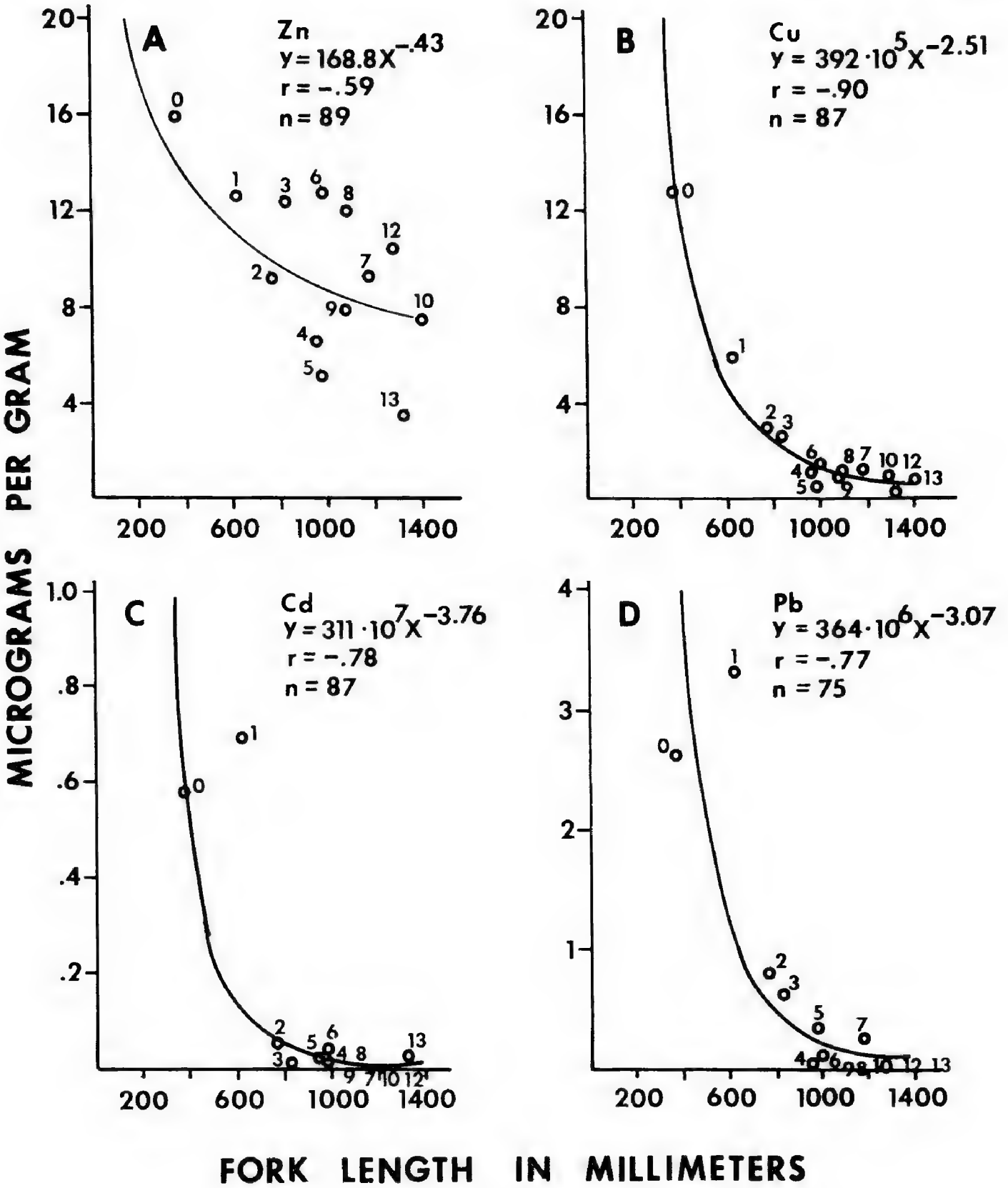


FIG. 1. Relationship between mean heavy metal concentration in otoliths and mean fork lengths of king mackerel.

(A) zinc
(B) copper
(C) cadmium
(D) lead

Numbers in figure are age in years at mean fork length.

examination of the internal structure of the otoliths is warranted (see Calaprice, McShaffrey and Lapi 1971 and Lapi and Mulligan 1981 for reviews of this approach).

LITERATURE CITED

ANONYMOUS. 1986. *Statgraphics*. Version:2.0, Computer program for IBM. S.T.S.C. Inc., Statistical Graphics Corporation.

BROTHERS, E.B., C.P. MATHEWS and R. LASKER. 1976. Daily growth increments of otoliths from larval and adult fishes. *Fishery Bulletin*. **74(1)**:1-8.

CALAPRICE, J.R., H.B. McSHAFFREY and L.A. LAPI. 1971. Radioisotope x-ray fluorescence spectrometry in aquatic biology: a review. *Journal of the Fisheries Research Board of Canada*. **28**:1583-1594.

CROSS, F.A., L.H. HARDY, N.Y. JONES and R.T. BARBER. 1973. Relation between total body weight and concentrations of manganese, iron, copper, zinc and mercury in white muscle of bluefish (*Pomatomus saltatrix*) and a bathyl-demersal fish (*Antimore rostrata*). *Journal of the Fisheries Research Board of Canada*. **30(9)**:1287-1291.

DANNEVIG, E.H. 1956. Chemical composition of the zones in cod otoliths. *Journal du Conseil Permanent International pour l'Exploration de la Mer*. **21(2)**:156-159.

DEGENS, E.T., W.G. DEUSER and R.L. HAEDRICH. 1969. Molecular structure and composition of fish otoliths. *Marine Biology*. **2**:105-113.

EMMEL, R.H., J.J. STOER and D.L. STUX. 1977. Atomic absorption methods manual, V. 1. *Standard conditions for flame operation*. Instrumentation Laboratory Inc., Analytic Instruments Division, Wilmington, Maine.

GAULDIE, R.W., E.J. GRAYNOTH and J. ILLINGWORTH. 1980. The relationship of the iron content of some fish otoliths to temperature. *Comparative Biochemistry and Physiology*. **66A**:19-24.

———— and A. NATHAN. 1977. Iron content of the otoliths of tarakihi (Teleosti: Cheilodactylidae). *New Zealand Journal of Marine and Freshwater Research*. **11(2)**:179-191.

HALL, R.A., E.G. ZOOK and G.M. MEABURN. 1978. National Marine Fisheries Service survey of trace elements in the fishery resource. National Oceanic and Atmospheric Administration. Technical Report. National Marine Fisheries Service. *Special Scientific Report-Fisheries*. **721**. 313 p.

IMMERMAN, F. 1908. Beitrage sur Altersbestimmung der Fische, 11, Die innere struktur der Schollenotolithen. *Wissenschaftliche Meeresuntersuchungen, Abteilung Helgoland*. **8**:129-176.

JOHNSON, A.G., W.A. FABLE, Jr., M.L. WILLIAMS and L.E. BARGER. 1983. Age, growth and mortality of king mackerel, *Scomberomorus cavalla*, from the southeastern United States. *Fishery Bulletin*. **81(1)**:97-106.

LAPI, L.A. and T.J. MULLIGAN. 1981. Salmon stock identification using a microanalytic technique to measure elements present in the freshwater growth region of scales. *Canadian Journal of Fisheries and Aquatic Sciences*. **38**:744-751.

MACPHERSON, E. and M. MANRIQUEZ. 1977. Variaciones de algunos elementos constituyentes del otolito y sus relaciones con el crecimiento do *Merluccius capensis*. *Investigacion Pesquera*. **41(2)**:205-217.

MEABURN, G.M. 1979. Heavy metal contamination of Spanish mackerel, *Scomberomorus maculatus*, and king mackerel, *S. cavalla*. In E.L. Nakamura and H.R. Bullis, Jr. (eds.), Proceedings: Colloquium on the Spanish and king mackerel resources of the Gulf of Mexico. Gulf States Marine Fisheries Commission, No. **4**:61-66.

MUGIYA, Y. 1964. Calcification in fish and shell-fish III, seasonal occurrence of a prealbumin fraction in the otolith fluid of some fish, corresponding to the period of opaque zone formation in the otolith. *Bulletin of the Japanese Society of Scientific Fisheries*. **30(12)**:955-961.

————. 1974. Calcium-45 behavior at the level of the otolithic organs of rainbow trout. *Bulletin of the Japanese Society of Scientific Fisheries*. **40(5)**:457-463.

NAKAMURA, E.L. and H.R. BULLIS, Jr. (eds.). 1979. Proceeedings: Colloquium on the Spanish and king mackerel resources of the Gulf of Mexico. Gulf States Marine Fisheries Commission, No. **4**. 117 p.

PANNELLA, G. 1971. Fish otoliths: daily growth layers and periodical patterns. *Science*. **173**:1124-1127.

PAPADOPOULOU, C., G. KANIAS and E. MORAITOPOULOU-KASSIMATI. 1976. Zinc content in otoliths of *Scober japonicus colias* from the Aegean Sea, versus age and total body length. In *Protection du littoral Mediterranee*, Premiere Partie, IIIes Journees Etudes Pollutions, pp. 69-73, Split, Commission Internationale pour l'Exploration Scientifique de la Mar Mediterranee.

———, ——— and ———. 1978. Zinc content in otoliths of mackerel from the Aegean. *Marine Pollution Bulletin.* **9(4)**:106-108.

———, ——— and ———. 1980. Trace element content in fish otoliths in relation to age and size. *Marine Pollution Bulletin.* **11(3)**:68-72.

REIBISCH, J. 1899. Ueber die Eizahl bei *Pleuronectes platessa* und die Altersbestimmung dieser Form aus den Otolithen. *Wissenschaftliche Meeresuntersuchungen, Abteilung Kiel, N.F.* **4**:233-248.

SIMKISS, K. 1974. Calcium metabolism of fish in relation to ageing. In T.B. Bagenal, (ed.), *The ageing of fish*, Proceedings of the International Symposium on the Ageing of Fish. University of Reading, England. pp 1-12, Unwin Bros., Ltd. England.

TRENT, L., R.O. WILLIAMS, R.G. TAYLOR, C.H. SALOMAN and C.H. MANOOCH III. 1983. Size, sex ratio, and recruitment in various fisheries of king mackerel, *Scomberomorus cavalla*, in the southeastern United States. *Fishery Bulletin, U.S.* **81(4)**:709-721.

VINOGRADOV, A.P. 1953. *The elementary chemical composition of marine organisms.* Memoir **11**. Sears Foundation for Marine Research, New Haven, Yale University. 647 p.

Contributions in Marine Science. (1989) Vol. 31:25–37.

A BIOLOGICAL AND PHYSIOLOGICAL CHARACTERIZATION OF THE RIO CARRIZAL ESTUARY, TAMAULIPAS, MEXICO

S.C. Rabalais[1], W.M. Pulich, Jr.[3], N.N. Rabalais[1], D.L. Felder[2], R.K. Tinnin, and R.D. Kalke

The University of Texas
Marine Science Institute
Port Aransas, Texas 78373

ABSTRACT

The Rio Carrizal estuary may constitute the northernmost tropical estuarine system in the western Gulf of Mexico. This report is a characterization of the biological and hydrographical aspects of this estuary from a point near its opening into the Gulf of Mexico to brackish waters upstream (24 km). The hydrography of the river, along with changes in bottom substrates and shoreline characteristics, combine to produce a gradient of tropical flora and fauna up the estuary.

Tropical seagrass beds, mangrove thickets and brackish water marsh comprise three major hydrophyte habitats found along the lower 15 km of the estuary. Shoreline and benthic samples of macroinvertebrates suggest that faunal assemblages of the Rio Carrizal are tropical in character but comprised substantially of western Gulf endemic species.

INTRODUCTION

Description of Region

South of the Rio Soto la Marina and north of the Rio Tamesi-Panuco, the coast of Tamaulipas is a region characterized by low mountains and small, ephemeral drainage basins. Perhaps the most tropical of these basins is the Rio San Rafael-Carrizal (Fig. 1). The San Rafael begins in the Sierra Tamaulipas, a long anticlinal arch formed principally of lower Cretaceous or Commanche limestone (Ordonez 1936). Near the base of these mountains, the river forms a small lake behind the Republica de Espana Dam before it flows into the Rio Carrizal (Fig.1). The Rio Carrizal then flows the remainder of the 25 km from its junction with the Rio San Rafael to the Gulf of Mexico

[1] Louisiana Universities Marine Consortium, Chauvin, Louisiana 70344
[2] Department of Biology and Center for Crustacean Research, University of Southwestern Louisiana, Lafayette, Louisiana 70504
[3] Resource Protection Division, Texas Parks and Wildlife, 4200 Smith School Road, Austin, Texas 78744

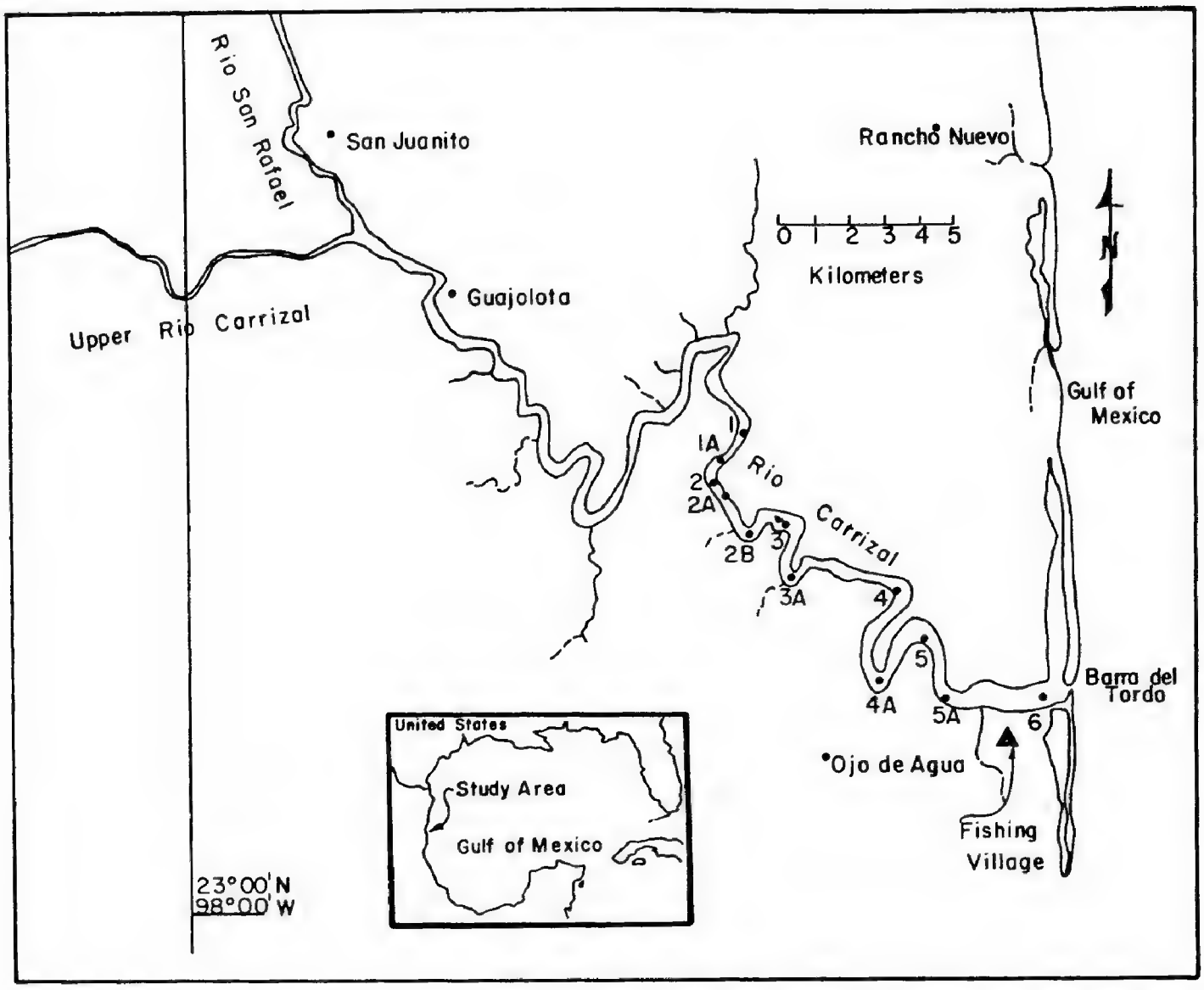


FIG. 1. The Rio Carrizal from its junction with the Rio San Rafael to Barra del Tordo. The locations of Stations 1–6 are indicated.

through isolated hills and low mountains of the Sierra de los Maratinas and the Sierra San Jose de las Rusias (Ordonez 1936). The principal vegetation along stream beds and in higher elevations of these mountains is tropical deciduous forest (Leopold 1950). Along the Rio Carrizal, deciduous forest extends all the way to the coast where it also surrounds the estuary formed by lower reaches of the river.

The Rio Carrizal is located on the boundary of the Koeppen's Cfa (humid subtropical) and Aw (tropical wet and dry) climatic areas (West and Augelli 1966). In a modification of the Koeppen system of classification, Garcia (1973) placed this system (identified as Lagona Chilillo) along with Laguna Morales to the north in the BS1 (h′) hw″ climatic area. North of Laguna Morales, the Laguna Madre, located in the BS1 (h′) hx″ climatic area (Garcia 1973), is characterized by low annual precipitation (250-700 mm/yr) and porous limestone surface sediments (Contreras 1985). Thorny semi-deciduous upland brush and a single species of intertidal mangrove, *Avicennia nitida* (=*germinans*), intertidally are the dominant vegetation of this region (Contreras 1985).

Vegetation along the Rio Carrizal is more characteristic of the low deciduous forest which is the dominant vegetation in the more tropical regions to the

south. Tiznado and Saldana (1980) reported three species of mangrove, the black [*Avicennia nitida* (=*germinans*)], red (*Rhizophora mangle*) and "mangle prieto" (probably a common name for the white mangrove *Laguncularia racemosa*) in Laguna de San Andres. This estuary is only about 50 km to the south of Rio Carrizal but is considered by Garcia (1973) to be typical of the AW1 climatic region.

The location of the Rio Carrizal in a transition region between two climatic areas, as well as the atypical physiography and vegetation associated with the river as it courses to the Gulf of Mexico, creates a unique estuarine setting in the Tamaulipan Biotic Province. Yet, this and adjacent coastal systems remain poorly characterized in the literature.

Study Area

Situated in the southeastern corner of the state of Tamaulipas near 23° 48′ W, the Rio Carrizal drains substantial portions of the eastern Sierra Tamaulipas slope rain forest. Its sinuous course is not intersected by major tributaries, and streams which enter the river flow intermittently. The steep banks of the river have been carved from sedimentary rock, but point bars, sandy beaches, and small islands have formed in the numerous bends along the river. Sediment in the river grades from coarse sand and gravel aggregate upriver to fine sand mixed with silt in the lagoon at the mouth of the river. Depth varies from < 1 m to 7.8 m. Most deeper areas are formed by scouring in bends of the river.

The lagoon at the mouth of the estuary is approximately 3 km long and 0.6 km wide. Arms of the lagoon, little more than mud flats at low tide, stretch approximately 6.5 km north and 4.5 km south, with barrier island spits forming their seaward margins. The lagoon opens to the Gulf of Mexico through Barra del Tordo, a natural pass. This pass is alternately opened and closed depending on climatic conditions, amount of freshwater inflow, and storm tides. When closed the estuary is isolated from the open Gulf of Mexico. An extended period of closure (4 years) occurred in the early 1960's during drought conditions (H. H. Hildebrand, personal communication). The closing of the pass in 1979 by Hurricane Anita prompted the Mexican government to open a new pass into the lagoon approximately 0.5 km north of the natural opening. This pass was open in May 1982 when our study was conducted, but appeared in the process of closing rapidly.

The only major settlement along the course of the river is a small fishing village on the southern shore of the lagoon. The major industry in this village is fishing. Oysters, crabs, mullet, a few snook, and small bait fish are taken from the lagoon, but the majority of the fish marketed are taken from offshore rock reefs.

METHODS AND MATERIALS

Over the last 10 years, we (SCR, NNR, DLF) have made several trips to the vicinity of Rio Carrizal and nearshore Gulf of Mexico waters to study the flora and fauna of this region. In May 1982, we

organized a team of marine scientists for a more comprehensive investigation of the Rio Carrizal estuary. Studies were conducted from 23-25 May 1982 and included a variety of physiographic and biological observations.

We selected 12 stations along a 24 km stretch of the estuary from the most upstream reaches navigable by a 5 m boat to the mouth near Barra de Tordo (Fig. 1).

Hydrographic measurements—water temperature, pH, dissolved oxygen and conductivity—were made with an Environmental Data Systems Series 4000 hydrolab. These measurements were made at 1-m interval depths at all stations on 24 May and at stations 1, 2, 3, 4, 5 and 6 on 25 May. Dissolved nutrients and water column chlorophyll *a* were determined on replicate water samples from the surface and 1 or 2 m depth. These samples were taken at stations 2, 3 and 5A on 25 May, fixed in the field, and analyzed according to the methods described by Pulich and Rabalais (1986).

The faunal component of the Rio Carrizal estuary was described from zooplankton samples, benthic cores, and random macrofaunal samples from shallow water and shore margins. Zooplankton tows were taken just below the surface for 1-min intervals with a #10 (153 μ) mesh net with a 0.5 m opening. The amount of water filtered was measured with a General Oceanic Model 2030 digital flowmeter. The duplicate samples were preserved with 5% buffered formalin. The presence of scyphozoans and ctenophores was noted in the field and these organisms removed from the samples by adding Chlorox. Samples were analyzed in the laboratory according to standard zooplankton techniques. Standing crops were expressed as a total number of individuals per m^3 of water. Zooplankton samples were taken at stations 1, 2, 3, 4, 5 and 6 on 25 May.

Benthic cores (7.5 cm diameter and 20 cm deep) were taken at 1 m depth along the banks adjacent to hydrographic station. The contents of the cores were washed through a 0. 5 mm mesh screen and preserved in 10% formalin containing rose bengal as a vital stain. These samples were returned to the laboratory where the organisms were identified to the most specific possible taxon and counted.

Invertebrate macrofaunal samples were taken as random collections from rocks and heavily-fouled mangrove roots, in shallow water near the edge of the river and at near shore intertidal and upper tidal terrestrial habitats on exposed river banks and vegetated upper shores. The location of shoreline and submerged vegetation was noted and vegetation samples were taken at each of the stations.

Species diversity (H″) of zooplankton and benthic communities was determined by a modified Shannon-Weiner index (Pielou 1966).

RESULTS

Physical data

Hydrographically, the Rio Carrizal is a graded, highly stratified estuary (Fig. 2). Surface water salinities ranged from 21.14‰ at the station nearest the Gulf of Mexico to brackish water (2.04‰) at the most upriver station. Salinities increased with depth throughout the estuary and were highest in bottom waters at the deepest stations (*e.g.* station 2B, salinity = 30‰+). At station 6, the water column was homogeneous with respect to salinity. Shallow upstream reaches of the study area (stations 1-2A) exhibited inverse thermal stratification, with a pronounced thermocline in the upper meter of the water column; highest temperature (33°C+) was recorded near bottom at a depth of 2 m (station 1). A positively heterograde temperature profile was evident at station 2B-4 with highest temperature (31-33°C) near 2 m depth, and lowest temperature at bottom; at the deepest station (2B) minimum temperature of

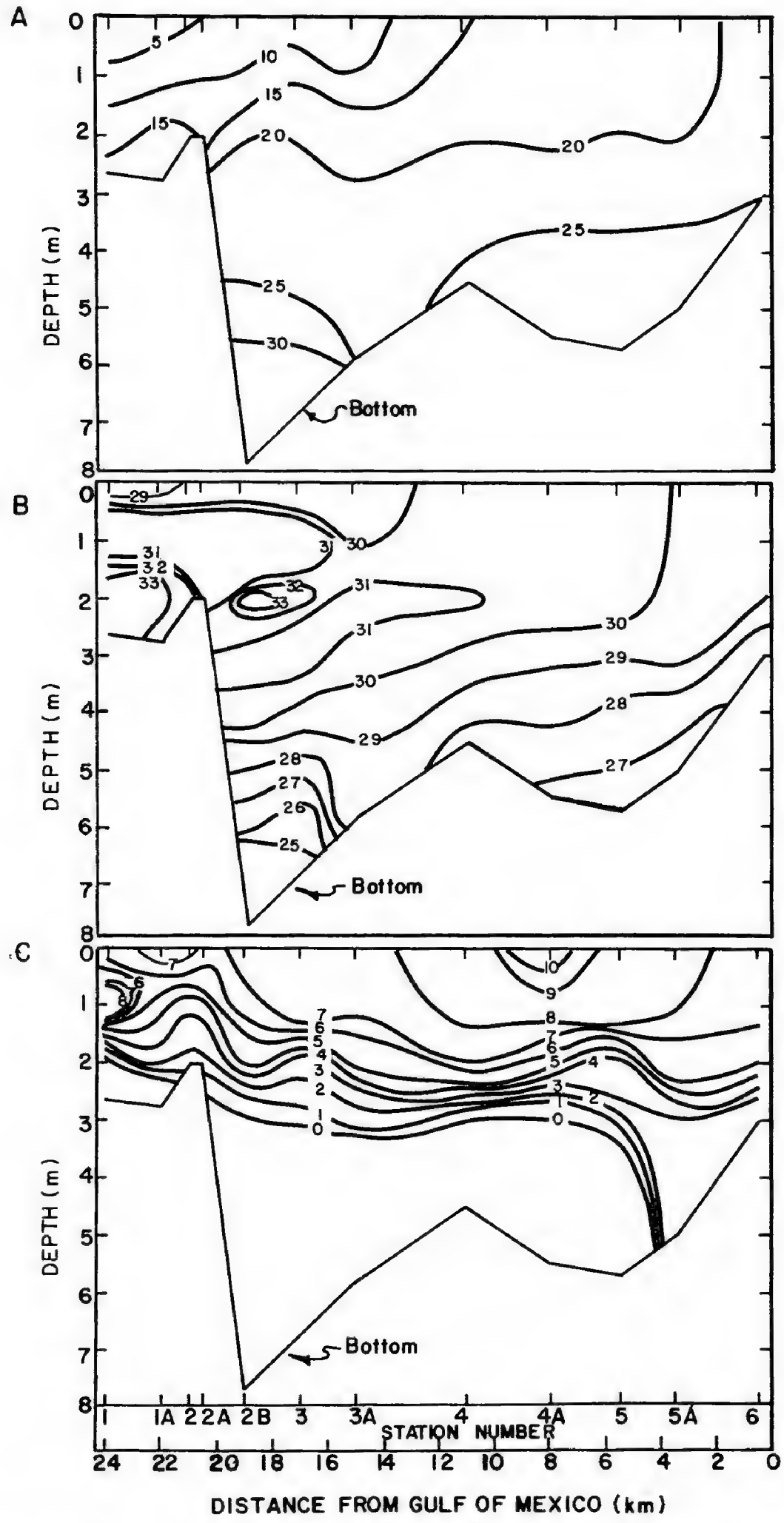


FIG. 2. Hydrographic data from Stations 1–6, a) salinity (‰) b) temperature (°C); c) dissolved oxygen (ml/l).

less than 25°C was recorded below a depth of 7 m. The upper water column (2 m) was mixed at stations 6, 5A and 4A, and graded to slightly lower temperature at depth. Water column pH decreased with depth and exhibited the greatest range at stations 2B and 3 where it decreased from 8+ at the surface to below 7 near the bottom (6.75 m). There was little variation in pH at the stations nearest the Gulf of Mexico (stations 6 and 5A). Except at station 1, dissolved oxygen also decreased with depth at all stations, with surface highs ranging from 7-10 ml/l. Anoxic waters were encountered below about 3 m at almost all stations except those near the mouth of the river. Secchi disc readings indicated moderately turbid waters, and ranged from 86 cm at station 1 to 137 cm at stations 3A and 5.

The eutrophic nature of the estuary was reflected in the water nutrient measurements (Table 1). Ammonia levels were typical of an estuary with high organic input and ranged from 4.2 μM on the surface at station 2 to 9.9 μM in 2 m of water at station 5A. Concomitantly, nitrate levels were low (< 0.05 μM) at all stations. Phosphate levels varied from a surface concentration of 5 μM at station 5A to 7.1 μM in 1 m of water at station 2. Chlorophyll *a* levels ranged from 10 μg/l at station 5A to 94 μg/l in 2 m depth at station 4.

Flora

Four different vascular plant communities were found growing in and along the river's edge: tropical deciduous forest, brackish water marsh, mangrove thicket, and seagrass beds. Three species of mangrove, black

TABLE 1

Ammonia, nitrate, phosphate and chlorophyll *a* measurements from stations 2, 4, and 5A. Replicate measurements of ammonia and phosphate are included for all stations, all depths. Nitrate and chlorophyll *a* measurements were not replicated.

Station	Sample Depth	Ammonia (μM)	Nitrate (μM)	Phosphate (μM)	Chlorophyll a (μg/l)
2	Surface	4.5	0.05	6.0	28
		4.2		5.9	
	1 m	6.1		5.9	37
		4.8		7.1	
4	Surface	5.2	0.05	5.7	20
		6.4		5.6	
	2+ m	5.2		5.8	94
		6.2		5.6	
5A	Surface	4.7	0.05	5.0	10
		6.4		6.4	
	2 m	9.0		5.3	20
		9.9		5.4	

(*Avicennia germinans*), red (*Rhizophora mangle*), and white (*Laguncularia racemosa*), were found growing along the banks of the river in the classical ecological relationship of other tropical lagoons (Thom 1967). Red mangroves, with their characteristic prop roots forming a water-front understory, grew in the shallow water at the edge of the estuary. Black mangroves (4-8 m in height) grew behind this red mangrove fringe on more elevated ground. White mangroves were found occasionally interspersed with black and red mangroves. The mangrove communities comprised the dominant aquatic vegetation from stations 6 to 3. Red and white mangroves were found as far upstream as station 2B (surface salinity 6.05‰) and black mangroves were found upstream of station 1A (surface salinity 3.15‰).

At stations 1 and 2A halophytic herbs (primarily *Borrichia frutescens* and *Batis maritime*) and grasses (*Paspalum vaginatum* and *Phragmites communis*) dominated the riparian plant community. These species were well-established along point bars, islands, and other locations where alluvial sediments accumulated along the river banks. Between stations 1 and 2 upstream, localized patches of alligator weed (*Alternanthera philoxeroides*) were observed in quite shallow waters near the river bank.

Submergent vegetation occurred in the lagoon behind the barrier island (station 6) and upriver at station 5A where *Halodule wrightii* covered 20 acres (200-300 g dry weight/m^2) in 0.1-0.3 m of water. A few sprigs of *Ruppia maritima* were found floating at station 5A, but rooted material was not located.

Macrophytic algae were not common upriver beyond station 5A, although a single sample of *Ectocarpus* sp. was found on a live oyster at station 3. At the brackish water stations (1, 2) filamentous green algae (Order Cladophorales) were occasionally found attached to vegetation and submerged sticks. Higher up the slopes of the river bank, beyond the brackish water marsh and mangrove zone, tropical deciduous vegetation occurred; *Acacia* sp. and ebony dominated in that habitat.

Fauna

As with the plant communities, there was a predictable salinity-associated gradation of the invertebrate fauna along the estuary. Zooplankton species diversity (H″) and total number of species were highest in the saline waters at the mouth of the estuary (Table 2). Standing crop, on the other hand, was high at all stations except station 1 where the lowest salinities were recorded and station 4 where ctenophores and *Aurelia* sp. occurred. *Acartia tonsa* was the dominant zooplankter at all stations but contributed most to the total number of individuals at upriver sites. Zoeae of the river shrimp *Macrobrachium* sp. were collected only at station 1. *Paracalanus crassirostris, Upogebia* sp. zoeae, *Sagitta* sp. (Table 2), *Pseudodiaptomus coronatus, Euterpinna acutifrons* and *Oikopleura* sp. were common at the most marine stations. Gammarid amphipods, *Cymadusa compta, Gammarus mucronatus* and *Ampelisca abdita* and the harpacticoid copepod *Metis* sp. were collected at station 6. These species are commonly associated with seagrass beds.

TABLE 2

Total number (no.) of zooplankton species /m^3, species diversity (H″), standing crop, and total number of selected zooplankton species for stations 1–6, 25, May 1982.

Station	1	2	3	4	5	6
Total no. species	17	16	14	16	19	36
Species diversity (H″)	.26	.03	.07	.70	1.60	1.95
Standing crop (total no. of individuals/m^3 x 100)	2,572	87,914	58,601	4,001	23,090	46,046
no./m^3 of dominant species						
Acartia tonsa	2,496	87,722	58,220	3,178	15,867	27,652
(% of species present)	(97.1)	(99.8)	(99.4)	(78.0)	(68.7)	(60.1)
Upogebia sp. zoea	0	3	170	68	47	244
Sagitta sp.	0	0	51	140	900	191
Paracalanus crassirostris	0	0	0	13	2,733	8,696

Core samples along the length of the lower Rio Carrizal indicated changes in species composition, and dominance and diversity in the benthic community (Table 3). Species diversity (H″) increased down river to station 4; decreased at station 5 and then increased slightly at station 6. Some benthic species such as the polychaete *Streblospio benedicti* sp., *Sphaeroma* sp., *Corophium* sp., and insect larvae found at upriver stations were not collected at stations near the mouth of the estuary. *Neritina virginea, Spio pettiboneae, Parandalia* sp., *Munna* sp., and *Parahesione luteola* were collected only at stations 5 and 6 nearer the mouth of the estuary. Other species were collected at stations along the length of the river. *Mediomastus californiensis* was collected at 5 of the 6 stations sampled and was a dominant species at 3 of these stations. *Grandidierella bonierroides* was collected at 4 stations but was a dominant organism only at station 3. Only two species, *Mediomastus californiensis* and *Upogebia affinis*, were among the most dominant species at more than one station. Juveniles and adults of two decapod crustaceans, *Callianassa louisianensis* and *Upogebia affinis* were collected in benthic cores at some of the same stations where the zoeal stages were common in the zooplankton samples. Most of the species collected in the benthic cores are common estuarine species throughout the Tamaulipan Biotic Province. However, the polychaetes *Parandalia* sp. (a dominant species at station 4), and *Cabira incerta*, have never been reported from this region. Other species,

TABLE 3

Number of species, density (no./m^3), total no. of individuals/m^3, species diversity (H″), and taxa of macroinvertebrates from all core samples combined at stations 1–6, 25 May 1982.

Station	**1**	**2**	**3**	**4**	**5**	**6**
Number of species	4	10	7	8	7	8
Density (no./m^3)	3.5	4.5	1.8	1.8	5.1	5.6
Total no.of individuals/m^3	40	51	20	22	58	63
Species diversity (H″)	.79	1.06	1.60	1.85	1.22	1.37
Polychaetes						
Mediomastus californiensis	*	-	0	*	*	0
Streblospio benedicti	*	-	-	-	-	-
Nereidae	-	0	0	-	-	-
Pectinaria gouldii	-	-	-	*	-	-
Parandalia sp.	-	-	-	*	0	-
Cabira incerta	-	-	-	0	-	-
Spiochaetopterus costarum	-	-	-	0	-	-
Chaetopteridae	-	-	-	0	0	-
Parahesione luteola					0	-
Capitellidae	-	-	-	-	0	-
Crustaceans						
Callianassa louisianensis	0	-	-	-	-	-
Hemicyclops sp.	-	0	-	-	0	-
Podocopid ostracod	-	0	-	-	-	-
Callinectes sp. megalopae	-	0	-	-	-	-
Talitroidid amphipod	-	*	-	-	-	0
Edotea montosa	-	-	0	0	-	-
Grandidierella bonierroides	0	-	*	0	-	0
Upogebia sp.	-	-	*	-	*	-
Mysidopsis bahia	-	-	-	-	-	0
Molluscs						
Crassostrea spat	-	*	-	-	-	-
Tagelus sp.	-	-	0	-	-	-
Neritina virginea	-	-	-	-	-	*
Miscellaneous						
Nemertea	-	-	-	-	0	-
Insect larvae	0	-	-	-	-	-

Taxa (presence 0, absence -, major dominant: > 10% of total no. of individuals *)

such as *Neritina virginea*, range no further north than the bays of extreme southern Texas.

The macrofaunal invertebrates collected in shallow water along the river banks and in shoreline areas (stations 1 to 6) graded from freshwater tolerant species to marine species. This gradation was most obvious in the decapod crustaceans which constituted the major component of the macroinvertebrates sampled, but was evident also in the non-decapods, particularly the molluscs. The gradation was primarily an additive phenomenon (Table 4), with the number of marine species increasing as samples were taken nearer the coast, and with most of the brackish or oligohaline species remaining a component of the assemblage (except at the most seaward station).

The decapod fauna at station 1 was composed of freshwater tolerant estuarine species - *Uca marguerita, U. spinicarpa, Sesarma cinereum, S. reticulatum, S. americanum, Callianassa louisianensis* and *Eurypanopeus depressus*. Similarly, the molluscan fauna was typical of oligohaline habitats *Polymesoda* sp., *Mytilopsis* sp., *Brachiodontes* sp., and *Neritina usnea.* At station 2, four additional decapods were found (*Upogebia affinis, Uca vocator, Aratus pisonii,* and *Callinectes sapidus*), as well as another mollusc (*Melampus* sp.). The collection of *Aratus pisonii*, the mangrove tree crab, at station 2 corresponded to the most upriver extent of black mangroves. At station 3 a few oysters (*Crassostrea*) and two additional decapod species (*Alpheus heterochaelis* and *Goniopsis cruentata*) were found. The first dense clumps of oysters were collected at station 4, along with many more species not present at upstream stations (Table 4). It was also at station 4 that the most upstream distribution of the marine scyphozoan, *Aurelia*, occurred. It was observed in

TABLE 4

Number of decapod crustacean species collected at each station along the Rio Carrizal estuary (see Fig. 1 for station locations) and number of species that were not collected at the adjacent upstream station.

Station Number	Number of Decapod Crustacean Species	Number of Decapod Crustacean Species Collected at a Station that were not collected at the adjacent Upstream Station
1	7	-
2	11	4
3	13	2
4	13	4
5/5A	21	6
6	29	23

the surface waters from station 4 to 6, and a dense aggregation was found in the bottom 1 m of water at station 4.

Oyster reefs heavily-fouled with barnacles, bryozoans, and hydroids were more extensive at the next downstream station (5). A number of xanthid crab species (*Panopeus lacustris, Panopeus simpsoni, Eurypanopeus depressus, Erytium limosum,* and *Menippe adina*) associated with the extensive oyster reefs and shallow subtidal and intertidal muddy shores, occurred at station 5, but not at station 4. The semiterrestrial species, *Cardisoma guanhumi, Ucides cordatus* and *Uca vocator*, were dominant along the higher river banks. The macroinvertebrate fauna attributed to station 6 was collected from a diversity of habitat types along the periphery of the lagoon and included seagrass beds, oyster reefs, intertidal mud flats, and less frequently flooded wind-tidal flats. Consequently, because of this diversity of the microhabitats and the marine nature of this station, a more diverse fauna was collected at station 6 for both decapod crustaceans (Table 4) and non-decapod species. Decapods from the vicinity of station 6 included a possibly undescribed (presumed endemic) species of *Callianassa* (nr. *C. guassutinga*) and a variant form of the pinnotherid crab *Pinnixa cristata*, which occurred as an apparent commensal of this mud shrimp (Manning and Felder 1988).

Collections of decapod crustaceans from the Rio Carrizal estuary, suggest that the macroinvertebrate fauna is more tropical in affinity than is the warm-temperate fauna of either the northern Gulf of Mexico or the Atlantic Carolinean. However, it is also characterized by the common occurrence of Gulf endemics, ranges of which may extend here from the northern Gulf of Mexico (*e.g. Menippe adina*; Williams and Felder 1986) or from the southwestern Gulf of Mexico (*e.g. Callinectes rathbunae* and *Uca marguerita*; Williams 1974; Barnwell and Thurman 1984). One endemic, *Uca subcylindrica,* is restricted to an area of the western Gulf of Mexico which roughly corresponds to the coastal and nearshore boundaries of the Tamaulipan Biotic Province from near Corpus Christi, Texas, to near Tampico, Mexico (Rabalais and Cameron 1983). Another, *Uca spinicarpa*, ranges broadly over the shores of the Gulf, both north and south of the Tamaulipan province.

DISCUSSION

The lower 24 km of the Rio Carrizal is a graded estuary which supports many tropical plant and animal species. In May 1982, the water column in this system was well-mixed 5.5 km from the pass at Barra del Tordo, but upstream from that point it was stratified and bottom waters in the deeper portions of the river were anoxic. Winds and tides were probably responsible for maintaining a mixed water column in the lower portion of the river. Tidal currents were observed pushing flotsam as far up river as station 4, and afternoon sea breezes would usually generate 0.25 to 0.5m swells in the lagoon. Farther up the estuary where tidal influence was less pronounced and the river was protected from the winds by its steep banks, a mixed water

column may be achieved during periods of peak river flow. Flow in the upper portions of the river was undetectable in May 1982.

Periodic flushing by fresh water, generally considered to be the sign of a healthy estuary (Cross and Williams 1981), may have never been common in this semi-arid region; however, it may have become even more infrequent as a result of the construction of the Republica de Espana Dam on the Rio San Rafael. The saber crab (*Platychirograpsus typicus*), and tarpon (*Megalops atlantica*), species common to less turbid freshwater streams and estuaries, were once common in the Rio Carrizal (H. H. Hildebrand, personal communication). These species were not observed during the present study.

Low standing crops of macroalgae were found at all points sampled along the river, despite the apparent availability of nitrogen in the form of ammonia. Low pH levels (which indicate high carbon dioxide content) in bottom waters also suggested that decomposition of organic material was actively occurring.

Even though the amount of fresh water entering the Rio Carrizal has been reduced by the damming of the Rio San Rafael, the graded nature of the fauna and flora is maintained along the length of the estuary. The increasing dominance of mangroves down river, along with the progressive addition of more-marine macroinvertebrate species, identify the Rio Carrizal as a graded estuary. The upper reaches were marked by the predominance of brackish water plants and animals in biological assemblages along the banks of the estuary. Changes in benthic macroinvertebrate species diversity (H′) from station 1 to station 6, with peak values at station 4, suggest the blending of low salinity and high salinity assemblages along the length of the estuary.

The dominance of estuarine zooplankton species (*e.g. Acartia tonsa*) and high standing crop values up river was indicative of low flow conditions during this survey. High flow conditions would result in the flushing of estuarine species down river, temporarily replacing them with lower salinity populations. An increasé in zooplankton species diversity (H′) from stations 2 to 6 was a result of increased numbers of marine species at the mouth of the river.

Perhaps the most unique aspect of the Rio Carrizal estuary is the tropical nature of its floral and faunal assemblages. In the Tamaulipan Biotic Province, the Rio Carrizal is the only system in which tropical forest communities have been reported contiguous to tropical marine communities. These marine communities are unique to the Tamaulipan Biotic Province and may represent the northernmost extension of many tropical species along the western coast of the Gulf of Mexico. Some of these tropical species may rarely range northward to the lower Texas coast but are not permanently established there because of colder climatic conditions. The mangrove thickets along the banks of the river are reminiscent of typical tropical mangrove associations found in the Laguna Terminos estuary (Thom 1967). The mangroves, in turn, support many of the tropical macroinvertebrate species collected along the shoreline stations. Superimposed on this tropical character, regional endemism in species assemblages of aquatic organisms may serve to further distinguish the system. This is evident in the decapod crustacean assemblages, and it remains to be seen whether similar patterns can be detected in other taxocenes.

The hydrography and biology of the Rio Carrizal estuary is probably influenced by seasonal fluctuations in freshwater inflow and the intrusion of salt water into the upper reaches of the estuary as a result of storm tides. To better understand this system, further investigations conducted on a seasonal basis will be necessary.

ACKNOWLEDGMENTS

We wish to thank the University of Texas Marine Science Institute and The University of Southwestern Louisiana for providing financial assistance for the collection and analysis of data and the Louisiana Universities Marine Consortium for final manuscript preparation.
The University of Texas Marine Science Institute Contribution Number 571.

LITERATURE CITED

BARNWELL, F.H., and C.L. THURMAN II. 1984. Taxonomy and biography of the fiddler crabs (Ocypodidae: Genus *Uca*) of the Atlantic and Gulf coasts of eastern North America. *Zoological Journal of the Linnean Society*. 81:23-87.

CONTRERAS, F. 1985. *Las lagunas costeras mexicanas*. Centro de Ecodessarrollo, Altadena 8, Mexico, 03810, D.F. 253 p.

CROSS, R. D. and D.L. WILLIAMS (eds). 1981. Proceedings of the National Symposium on Freshwater Inflow to Estuaries. U. S. Fish and Wildlife Service, Office of Biological Services. FWS/OBS-81/04. 2 volumes.

GARCIA, E. 1973. Modificaciones alsistema de clasificacion climatico de Koppen. In F. Contreras, *Las lagunas costeras mexicanas*. Centro de Ecodessarrollo Altadena 8, Mexico, 03810, D.F. (1985) 253 p.

LEOPOLD, A.S. 1950. Vegetation zones of Mexico. *Ecology*. 31(4):507-515.

MANNING, R.B., and D.L. FELDER. 1988. The *Pinnixa cristata* complex in the western Atlantic, with descriptions of the two new species (crustacea, Decapoda, Pinnotheridae). *Smithsonian Contributions to Zoology* (in press).

ORDONEZ, E. 1936. Principal physiographic provinces of Mexico. *Bulletin of the American Association of Geology*. 20(10):1277-1307.

PIELOU, E.C. 1966. Shannon's formula as a measure of specific diversity: its use and misuse. *American Naturalist*. 100:463-465.

PULICH, W., and S. RABALAIS. 1986. Primary production potential of blue-green algal mats on southern Texas tidal flats. *Southwestern Naturalist*. 31(1):39-47.

RABALAIS, N.N., and J.N. CAMERON. 1983. Abbreviated development of *Uca subcylindrica* (Stimpson 1859) (Crustacea, Decapoda, Ocypodidae) reared in the laboratory. *Journal of Crustacean Biology*. 3:519-541.

THOM, B.G. 1967. Mangrove ecology and deltaic geomorphology Tabasco, Mexico. *Journal of Ecology*. 55(2):01-343.

TIZNADO, A.L., and R. SALDANA P. 1980. Aportacion al conocimiento del compartaminto hidrobiologico de laguna de San Andres, Adama, Tamaulipas. Mem. II Simp. Latinoamer. Acvacultura. 375-392.

WEST, R.C. and J.P. AUGELLI. 1966. *Middle America Its Lands and People*. Prentice Inc. Englewood Cliff, New Jersey. 482 p.

WILLIAMS, A.B. 1974. The swimming crabs of the genus *Callinectes* (Decapoda:Portunidae). *Fishery Bulletin*. 72(3):685-798.

_____ and D.L. FELDER. 1986. Analysis of stone crabs: *Menippe mercenaria* (Say), restricted and a previously unrecognized species described (Decapoda:Xanthidae). *Proceedings of the Biological Society of Washington*. 99(3):517-543.

Contributions in Marine Science. (1989) Vol. 31:39–50.

OCCURRENCE, AGE AND GROWTH OF TWO MORPHOLOGICAL TYPES OF SAND SEATROUT (*CYNOSCION ARENARIUS*) LARVAE IN THE WINTER AND EARLY SPRING COASTAL WATERS OFF WEST LOUISIANA

James H. Cowan, Jr.,[1] Richard F. Shaw and James G. Ditty

Center for Wetland Resources
Louisiana State University
Baton Rouge, Louisiana 70803-7503

ABSTRACT

Two distinct morphological types (morphs A and B) of sand seatrout, *Cynoscion arenarius*, larvae were collected in west Louisiana coastal waters in the winter and early spring of 1981-1982. The two larval morphs were separable by three pigment differences:

1) the presence or absence of a melanophore on the dorsal midline (hypomere 16-17);
2) the number of melanophores on the preanal finfold; and,
3) the size of larvae at the initiation of lateral pigment formation.

Based on data obtained from growth analyses, both morphs were assumed to deposit daily growth increments in their saccular otoliths; the data were used to generate a linear growth equation for each by using analysis of covariance. Morph A grew significantly faster (0.20 mm d^{-1}) than morph B (0.14 mm d^{-1}). Combined length frequency and age-size at capture data indicate that sand seatrout spawning may have begun in December in 1981 but had definitely begun by early January 1982. The two morphs were separated in horizontal space and little overlap occurred in their distribution.

INTRODUCTION

The sand seatrout, *Cynoscion arenarius* (Ginsburg), ranges from southwest Florida (Roessler 1970) throughout the Gulf of Mexico (Gulf) to the Bay of Campeche, Mexico (Hildebrand 1955) and is among the most abundant fishes in Louisiana estuaries and in the shallow northern Gulf (Gunter 1945; Christmas and Waller 1973; Shlossman and Chittenden 1981; Herke, Rogers and Grimes 1984). Because of its abundance, sand seatrout are a major component of the northern Gulf recreational and commercial groundfish

[1] The University of Maryland, Center for Environmental & Estuarine Studies, Chesapeake Biological Laboratory, Solomons, Maryland 20688-0038

fishery landings (Roithmayr 1965; Gutherz, Russell, Serra and Rohr 1975; Shlossman and Chittenden 1981; Nakamura 1981). The current controversy over the fishery status of red drum (*Sciaenops ocellatus*) and spotted seatrout (*Cynoscion nebulosus*) may make the sand seatrout fishery even more important in the future.

Despite its abundance and importance, little life history information on sand seatrout is available (see Cowan 1985, for review). Early developmental stages of sand seatrout were first described by Daniels (1977). However, recently several authors have suggested that the taxonomic status between sand seatrout and weakfish, *Cynoscion regalis*, remains unclear and that literature on *C. regalis*, might apply to sand seatrout (Moshin 1973; Weinstein and Yerger 1976; Cowan 1985; Ditty 1989). Also in a recent study, Paschall (1986) could not separate Gulf of Mexico juvenile sand seatrout from Atlantic coast weakfish by using electrophoretic techniques. In addition, several studies (Ditty 1984; Cowan 1985; Ditty 1986) have collected two distinct morphological types (morphs) of sand seatrout larvae in Louisiana coastal waters.

Barger and Williams (1980) reviewed the literature on sand seatrout and stated that there were insufficient data for age and growth analyses. Shlossman and Chittenden (1981) examined the reproduction, movements and population dynamics of juvenile and adult sand seatrout in Texas waters and determined growth for fish 40 mm total length (TL) and larger. They suggested that annuli on scales could be used to age sand seatrout as accurately as length-frequency data even though Benefield (1971) reported that "clearly defined annuli were difficult to distinguish." No quantitative information has been published on age and growth of larval sand seatrout in northern Gulf coastal waters.

The objectives of this study were to:

1) briefly describe the pigment differences between morphs of sand seatrout larvae;

2) estimate larva growth rates from increments in saccular otoliths; and

3) use age-size at capture to estimate spawning time in Gulf coastal waters.

Possible explanations for the existence of the two larva morphs and for differences in their growth rates are discussed. Differences in larvae growth, morphology and pigmentation have been used diagnostically to compare lab-reared and wild larvae of the same species (Houde and Swanson 1975; Fukuhara and Kuniyuki 1978), to assess nutritional condition of larvae reared in the laboratory (Yin and Blaxter 1986) and captured in the sea (O'Connell 1980; Hewitt, Theilacker and Lo 1985; Theilacker 1986). Ontogenetic characters have been used to examine systematic relationships in many studies (Kendall, Ahlstrom and Moser 1984, for review). Pigment anomalies have also been used as a population character in plaice (*Pleuronectes platessa* L.) (De Veen 1969).

METHODS AND MATERIALS

Ichthyoplankton Collections

A total of 4,100 larval sand seatrout were collected during five mid-monthly cruises from December 1981 to April 1982 in west Louisiana coastal waters on a sampling grid consisting of 37 stations on five transects. The grid was located from west of Sabine Pass, Texas to east of the Mermantau River, Louisiana (Fig. 1). The two longest transects extended to the shelf break (200 km) and the others, which were about 65 km long, extended to the 18-m depth contour.

A 60-cm, opening and closing, paired "bongo type" BNF-1[2] plankton sampler fitted with 335 and 500 μm mesh nets was used for all collections. Sampling consisted of 10-minute stepped oblique tows from near bottom to surface at a retrieval rate between the five steps of approximately 20 m/min.

Larvae for pigment analyses (N = 250; 125 Morph A, 125 Morph B) were selected randomly from samples collected in March and April that were preserved in 10% buffered formalin in seawater in the field and later transferred to 4% buffered formalin. Larvae used for the age analyses (N = 149) were taken from the 500-μm nets at stations A-1, A-8, B-2, B-6, C-1, C-5, D-2, D-7, E-1 and E-8 (Fig. 1) in March and April and preserved in 100% isopropanol. To assure adequate preservation, the isopropanol was changed once within 48 h after returning to the laboratory.

Otolith Preparation and Age Determination

Otolith preparation and age determination was based on Taubert and Coble (1977). Saccular otoliths were removed, mounted in Permount on a glass microscope slide and, if sufficiently thick to prevent a direct increment count, ground in the sagittal plane with No. 600 ultra-fine silica-carbide sand paper until the core was reached. Otoliths were etched in 5% EDTA (ethylene dinitrilotetracetic acid) for 15-45 seconds, polished, covered by a cover slip, and observed using a polarized oil immersion light microscope at 400-1000×. Three independent increment counts were made on each otolith. To prevent bias, the reader was not made aware of the prior counts, the size of the larva or the morph. Replicate counts never differed by more than 7.5%, so the three counts were averaged to give a final estimate. Maximum otolith diameter and larvae TL were measured to the nearest 0.01 and 0.1 mm, respectively, with ocular micrometers in oil immersion and dissecting microscopes.

Estimation of Larvae Growth

Larva age was estimated by adding four to the number of otolith increments counted. Many marine fish larvae do not form otolith increments until the yolk-sac is absorbed (Brothers, Matthews and Lasker 1976; Campana 1984) and other sciaenids begin increment deposition four to five days after hatching (Peters, Devane, Boyd, Clements and Powell 1978; University of Texas Mariculture Program Report 1982-1983; Warlen and Chester 1985). Consequently, we added four days to account for yolk-sac absorption time even though Peters and McMichael (1987) reported increment deposition beginning on the day of hatch in sagittae of lab-reared larval red drum.

Linear growth models were used to examine the age and growth data for larval sand seatrout based on the work of Warlen (1981), Beckman and Dean (1984), Govoni, Chester, Hoss and Ortner (1985), Essig and Cole (1986), and Cowan (1988). Analysis of covariance (ANOCOVA) was employed to determine differences in growth rates between morphs and in the ratios of otolith diameter to larva TL and increment number.

---

[2] Tareq and Co., 8460 SW 68th Street, Miami, FL 33143

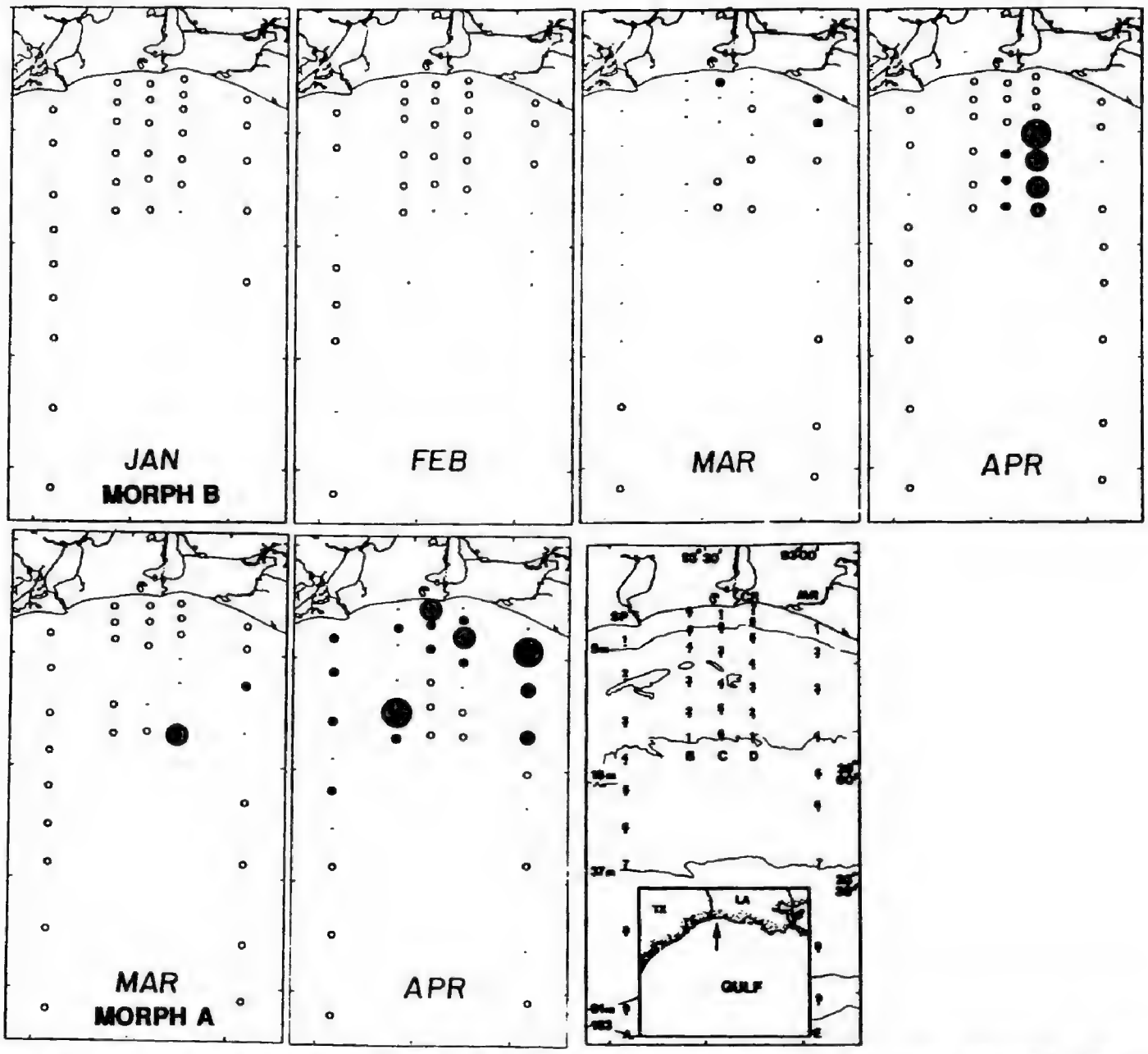


FIG. 1. Density and distribution of sand seatrout, *Cynoscion arenarius*, larvae by month, Jan to Apr 1982. The distributions are separated by morphological type. The densities are as follows:

○ = 0
· = 0-10
• = > 10-50
● = > 50-99
● = > 99-250
● = > 250

per 100 m^3 of water filtered from all plankton tow types. Also shown is sampling grid indicating station location and configuration including selected isobaths. SP = Sabine Pass, Texas; CR = Calcasicu River, Louisiana; MR = Mermentau River, Louisiana. Tick marks are 30 minute increments of latitude.

RESULTS

Pigmentation

Many of the sand seatrout larvae from the Gulf of Mexico possessed a melanophore on the dorsal midline opposite a large melanophore in the anal fin base typical of weakfish from the Atlantic. With increased larva size, the

dorsal melanophore was located near the posterior third of the dorsal fin base (hypomere 16-17; Ditty 1989). However, not all larvae possessed the dorsal melanophore; those that did not were classified as morph A. Larva morph A pigment characters were generally consistent with the series described by Daniels (1977) and clarified by Ditty (1989) for larvae up to 5 mm standard length.

Morph B larvae possessed all of the general external pigment characters described for morph A, with the following differences:

1) the presence of the dorsal melanophore;

2) the number of melanophores on the pre-anal finfold (morph A typically had one whereas morph B larvae > 5 mm TL always had two melanophores, and there were often three);

3) the size of larvae at initial lateral pigment formation. Larval sand seatrout morph A began lateral pigmentation at an average size of about 12 mm TL. Lateral pigment formation on morph B typically began when larvae were approximately 8 mm TL. Little over-lap of the characters described above occurred between the two morphological types. On occasion, the dorsal melanophore was not visible on small (< 3.5 mm TL) morph B larvae but the other characters could be used to separate the morphs, particularly in larvae greater than 5 mm TL.

Age and Growth

Sand seatrout (both morphs; $N = 149$) larvae examined for age analysis ranged from 2.2 to 11.1 mm TL and were estimated to be from 10 to 70 d old. The pooled linear growth equation was ($P < 0.0001$; $r^2 = 0.74$) $L_{(t)} = 0.173(t) + 1.480$ mm where $L_{(t)}$ = TL in mm and (t) = age in days (increment number + 4). Interpretation of ANOCOVA suggests that morph type A grew significantly faster than morph B (Table 1-A; Fig. 2). The growth equation of morph A ($N = 81$), useful to predict TL up to age 70 d, is $L_{(t)} = 0.197(t) + 1.220$ mm. The equation for morph B ($N = 68$), useful to predict TL to an age of 60 d, is $L_{(t)} = 0.142(t) + 1.459$ mm.

TL was regressed on saccular otolith maximum diameter to detect differences between morphs (Table 1-B). The regression slopes for morphs A and B were significantly different from zero. However, the intercepts and slopes were not significantly different between morphs so a pooled equation $L_{(D)} = 0.937(D) + 0.282$ where $L_{(D)} = \log_{10}$ at $\log_{10}$ otolith diameter (D), useful to predict relationships for both morphs from 2.5 to 11 mm TL, is appropriate. The model r^2 was 0.90 and the slope of the pooled regression did not differ significantly ($P > 0.05$) from unity.

Slopes of the regressions of increment number to otolith diameter were significantly different from zero and between morphs (Table 1-C). Otoliths of morph B larvae had more increments per unit diameter. This indicates that morph B otolith increments were narrower than morph A of similar age, suggesting slower growth or different rates of increment deposition. Otoliths from both morphs had no distinct or abrupt changes in increment width from the primordium to the distal edge.

TABLE 1

Summary data from analyses of covariance to detect differences in: (A) growth rates, (B) otolith diameter and (C) increment number between two morphs of sand seatrout, *Cynoscion arenarius*, larvae collected form January to April, 1982.

A. **Dependent variable: Larvae Total Length**		r^2=0.84
Source	*DF*	*PR > F*
Model	3	0.0001**
Age (slope = 0)	1	0.0001**
Morph A or B (same intercepts)	1	0.0001**
Age/morph (same slopes)	1	0.0001**
Error	146	
Corrected Total	149	
B. **Dependent variable: $\log_{10}$ Total Length**		r^2=0.90
Source	*DF*	*PR > F*
Model	3	0.0001**
$\log_{10}$ of otolith diameter (slope = 0)	1	0.0001**
Morph A or B (same intercepts)	1	0.0621 (*NS*)
$\log_{10}$ of otolith diameter/morph (same slopes)	1	0.1438 (*NS*)
Error	146	
Corrected Total	149	
C. **Dependent variable: Increment Number**		r^2=0.81
Source	*DF*	*PR > F*
Model	3	0.0001**
Otolith diameter (slope = 0)	1	0.0001**
Morph A or B (same intercepts)	1	0.0001**
Otolith diameter/morph (same slopes)	1	0.0490*
Error	146	
Corrected Total	149	

* Statistically significant ($PR < 0.05$)
** Highly significant ($PR < 0.01$)
(*NS*) Not significant

Spawning Time

All larvae collected in January and February ($N = 20$) were morph B; however, only one 3.9 mm TL larva was collected in January. Both morphs were collected in March ($N = 203$) and April ($N = 3{,}876$) (Fig. 1). The monthly modal lengths of morph B larvae in February and March were 2.5 and 5.5 mm TL, respectively. Based on our age and growth data, the morph B larva

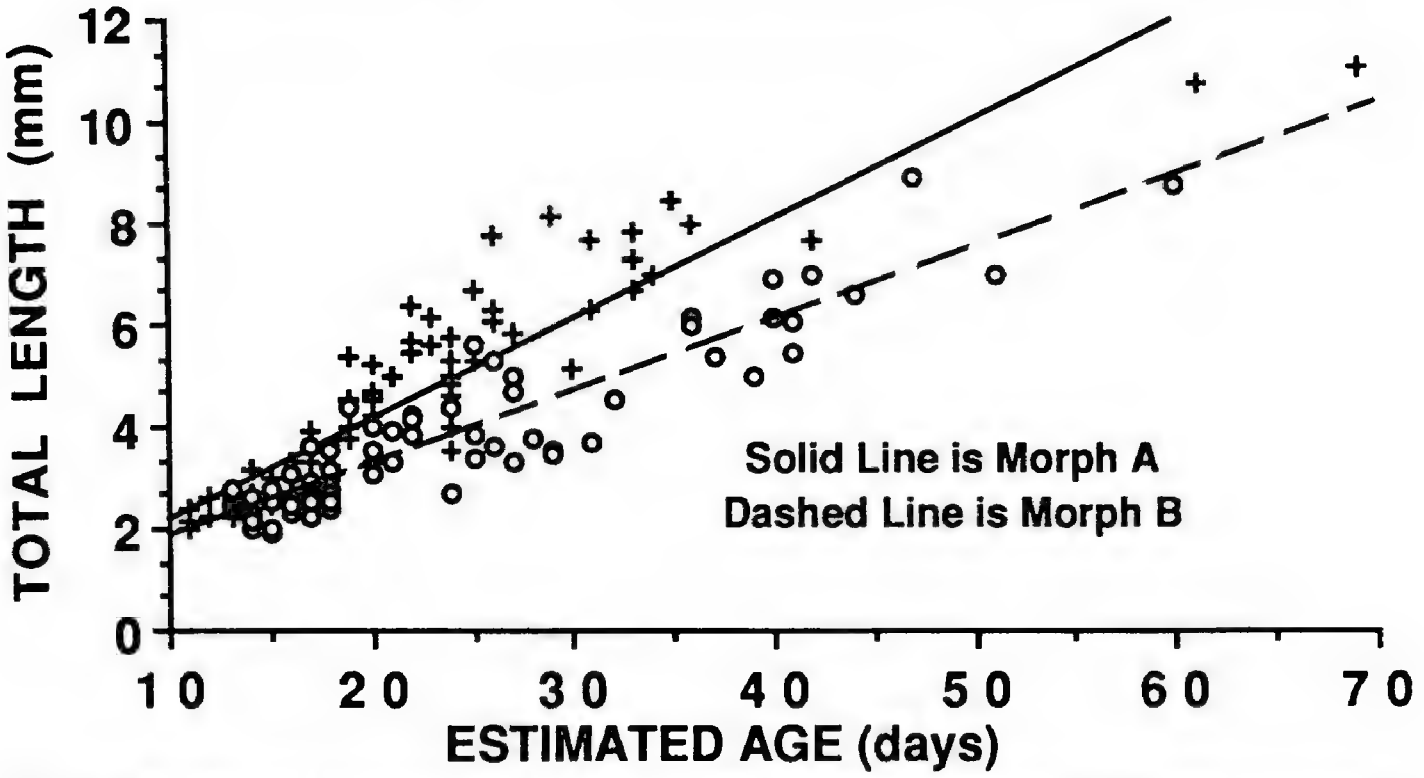


FIG. 2 Regression of larva total length (mm) on age (increment number + 4) at time of capture of larval sand seatrout.

collected in mid-January may have been as old as 24 to 25 d. This suggests limited spawning may have begun in December 1981. Larvae of the modal lengths in February and March were approximately 15 and 36 d old, respectively. Length-frequency data from all sand seatrout collected (N = 4,100), combined with information on larva age and growth, indicate spawning had definitely begun by early January 1982.

Interpretation of monthly modal lengths from April data is more complicated since many larvae of both morphs (2,283 morph A; 1,593 morph B) were collected. Most morph A larvae collected in March were small (Fig. 3) and the monthly modal length of 2.5 mm TL indicates larvae to be about 12 to 14 d old. In mid-April, the monthly modal length of morph A larvae was again 2.5 mm TL although larvae up to 17 mm TL were collected (Fig. 3). Based on the growth equation for morph A, a 17-mm TL larva would be approximately 90 d old and, therefore, would have been spawned in February.

The modal length of larval morph B decreased from March to April even though larvae up to 12.5 mm TL were collected. A modal length of 2.5 mm TL in April reflects the presence of many small larvae in the samples. However, a 12.5 mm larva would be approximately 85 d old, based on the growth equation for morph B.

Distribution

In general, sand seatrout larvae occurred inshore of mid-shelf (< 65 km offshore), primarily at depths between 10-25 m, and in the eastern portion of the study area (Fig. 1). Few were present at stations with depths greater than 25 m (Cowan and Shaw 1988). Larvae were captured in 66 of the 189

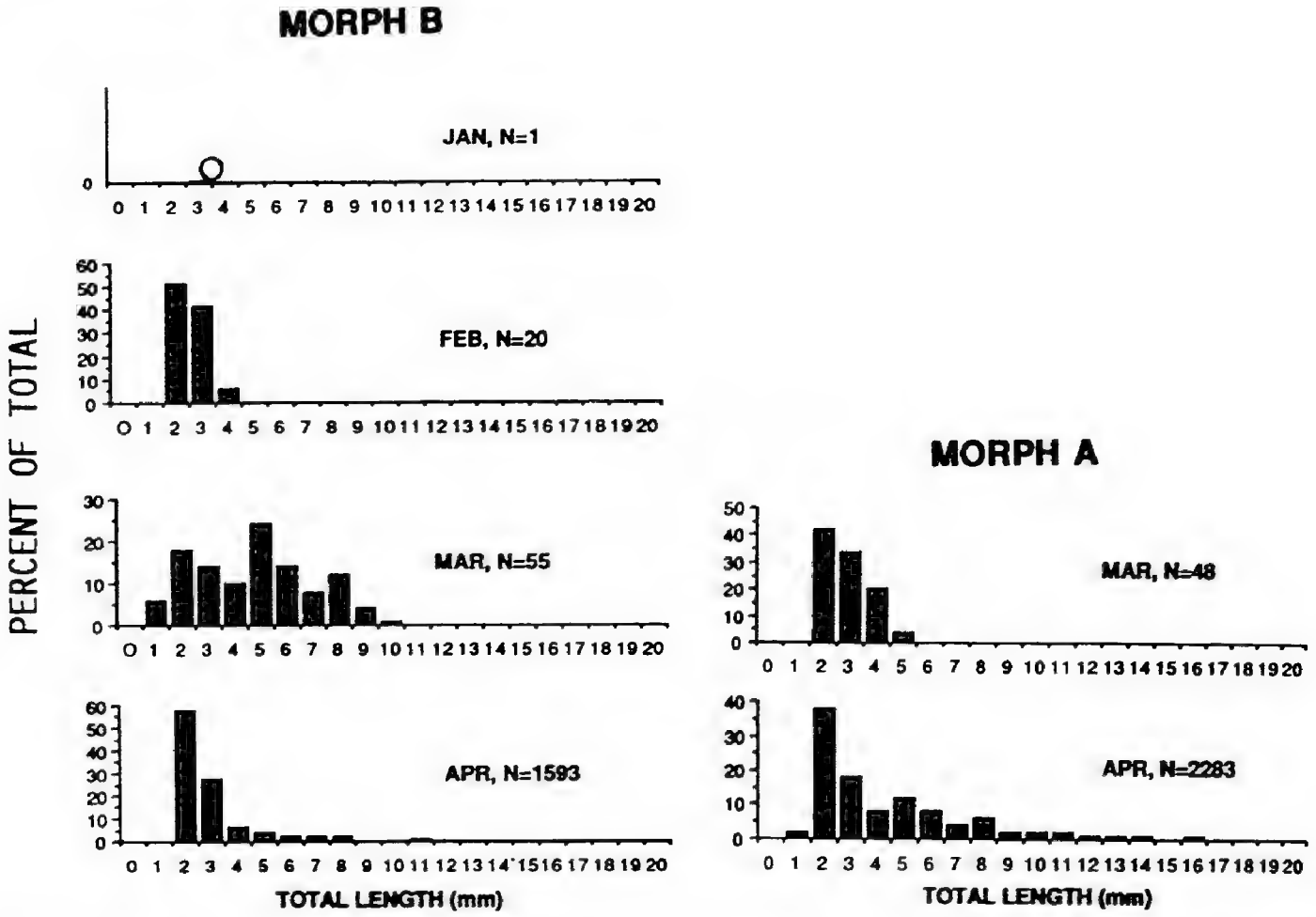


FIG. 3 Length-frequency data by month for sand seatrout, *Cynoscion arenarius*, morphological types A and B larvae. N = total number caught and measured. Only one Morph B larva was collected in January.

ichthyoplankton collections during this 5-month study. Morph A larvae were captured at 33 stations and morph B at 40 stations (Fig. 1). However, the two morphs occurred together only seven times at the 66 stations where larvae were collected. Cowan (1985) used available chemical, physical and biological data, including food abundance (zooplankton biomass), in a multivariate statistical analysis (canonical correlation) to attempt to identify water mass characteristics explaining the separation of the larval morphs, but none were identified. The two morphs were similar in their statistical lodgings (canonical factor scores) on several environmental variables collected concurrently with the ichthyoplankton (Cowan 1985, Chapter 4).

DISCUSSION

The distinct physiological (growth rate), ecological (spatial distribution) and morphological (pigment pattern) differences between the two morphs pose several questions: are they two species or subspecies, two distinct populations of the same species, hybrids, or a result of wide natural variation in the phenotype of one species exhibiting variation at the population level? As previously mentioned, the taxonomic status between *C. regalis* and *C. arenarius* is unclear. A recent study by Paschall (1986) showed that sand

seatrout from the Gulf were similar on 53 alleles at 21 loci to weakfish (*C. regalis*) (Nei's unbiased genetic identity similarity coefficient = 0.970) from Atlantic east coast waters and suggested the phylogenetic separation of the two is uncertain. Adult sand seatrout and weakfish cannot be separated meristically and Ginsburg (1929) noted the similarity between the two in his original description of *C. arenarius*. Sand seatrout (particularly morph B) and weakfish larvae exhibit very similar pigmentation and their reliable separation is not possible based on Daniels (1977) description of larval sand seatrout (Stender 1980; Ditty 1989). Daniels (1977) illustrated (Fig. 8) one 7.5 mm 1989 SL larva with the dorsal melanophore present (*i.e.*, morph B); the others she illustrated did not have dorsal melanophore (*i.e.*, morph A). This may account for Stender's (1980) inability to distinguish Gulf of Mexico sand seatrout larvae from those of the silver seatrout (*Cynoscion nothus*) and weakfish (*C. regalis*) from Atlantic east coast waters.

Although daily growth increments have not been validated in the sagittae of larval sand seatrout, they were found in otoliths of spotted seatrout, *Cynoscion nebulosus*, from the Gulf (McMichael and Peters, personal communication [3]). We assumed that increments in the saccular otoliths of larval sand seatrout from northern Gulf coastal waters also were deposited daily.

Interpretation of our data suggest that morph A grew significantly faster than morph B. However, the estimated daily growth rates of 0.197 mm d^{-1} for morph A and 0.142 mm d^{-1} for morph B. are within the ranges of those reported for laboratory reared *C. nebulosus* (Taniguchi 1979) and for other larval sciaenids (Warlen 1981; University of Texas Mariculture Program Report 1982-1983; Beckman and Dean 1984; Warlen and Chester 1985; Peters and McMichael 1987; Cowan 1988). Seasonal variation in growth rate due to differences in temperature between months was assumed to be small since most (~95%) of the larvae of both morphs used in the age analyses were collected in April at stations with surface temperatures ranging from 20-21°C.

It is known that environmental conditions in oceanic waters can vary sufficiently to cause wide variability in larvae condition and growth rates (Theilacker 1978; O'Connell 1980; Theilacker 1986). Even though the morphs were growing at different rates, neither morph appeared starved and Ditty (1989) found no significant between-morph differences in body proportions of preflexion larvae. These data are presently insufficient to determine the taxonomic significance of the two larval sand seatrout morphs but suggest the need for further taxonomic and population studies of Gulf of Mexico *Cynoscion*.

ACKNOWLEDGMENTS

We would like to thank Drs. B. Thompson, and J. Lyczkowski-Shultz for their interest and discussion during this study. We gratefully acknowledge Drs. E.D. Houde, R.E. Turner, and J.M. Fitzsimons for their critical review of this manuscript.

---

[3] State of Florida Department of Natural Resources, 100 Eighth Avenue, SE, St. Petersburg, FL 33701

Funding was provided by Louisiana Department of Wildlife and Fisheries, U.S. Department of Energy and LSU Center for Wetland Resources cooperative agreement No. DE-FC96-81P010313. Additional support was given by the LSU Department of Marine Sciences, Office of Sea Grant Development and the Coastal Fisheries Institute.
This is contribution no. LSU-CFI-86-14.

LITERATURE CITED

BARGER, L.E. and M.L. WILLIAMS. 1980. A summarization and discussion of age and growth of spot, *Leiostomus xanthurus* Lacepede, sand seatrout, *Cynoscion arenarius* Ginsburg, and silver seatrout, *Cynoscion nothus* (Holbrook), based on a literature review. NOAA Technical Memorandum NMFS-SEFC-14, 15 p.

BECKMAN, D.W. and J.M. DEAN. 1984. The age and growth of young-of-the-year spot, *Leiostomus xanthurus* Lacepede, in South Carolina. *Estuaries*. 48:487-496.

BENEFIELD, R.L. 1971. A study of sand seatrout (*Cynoscion arenarius* Ginsburg) of the Galveston Bay area. Texas Parks and Wildlife Department Coastal Fisheries Project Report 1969-1970. 225 p.

BROTHERS, E.B., C.B. MATTHEWS and R. LASKER. 1976. Daily growth increments in otoliths from larval and adult fishes. *Fishery Bulletin*. 74:1-9.

CAMPANA, S.E. 1984. Interactive effects of age and environmental modifiers on the production of daily growth increments in otoliths of plainfin midshipmen, *Porichthyes notatus*. *Fishery Bulletin*. 83:165-177.

CHRISTMAS, J.Y. and R.H. WALLER. 1973. Estuarine vertebrates, Mississippi. pp. 323-406. In J.Y. Christmas (ed) Cooperative Gulf of Mexico estuarine inventory and study, Mississippi. Gulf Coast Research Laboratory.

COWAN, J.H., Jr. 1985. The distribution, transport and age structure of drums (family Sciaenidae) spawned in the winter and early spring in the continental shelf waters off west Louisiana. Ph.D. Thesis, Louisiana State University., Baton Rouge 182 p.

_____. 1988. Age and growth of Atlantic croaker, *Micropogonias undulatus*, larvae collected in the coastal waters of the northern Gulf of Mexico as determined by increments in saccular otoliths. *Bulletin of Marine Science*. 42:349-357.

_____ and R.F. SHAW. 1988. The distribution, abundance and transport of larval sciaenids collected during winter and early spring from the continental shelf waters off west Louisiana. *Fishery Bulletin*. 86(1):129-142.

DANIELS, K. 1977. Description, comparison, and distribution of larvae of *Cynoscion nebulosus* and *Cynoscion arenarius* from the northern Gulf of Mexico. M.S. Thesis, Louisiana State University, Baton Rouge. 48 p.

de VEEN, J.F. 1969. Abnormal pigmentation as a possible tool in the study of the populations of the plaice (*Pleuronectes platessa* L.). *Journal de Conseil International pour Exploration de la Mer*. 32(3):344-383.

DITTY, J.G. 1984. Seasonality of sciaenids in the northern Gulf of Mexico. *Association of Southeastern Biologists Bulletin*. 31(2):55.

_____. 1986. Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality. *Fishery Bulletin*. 84:935-946.

_____. 1989. Separating early larvae of sciaenids from the western North Atlantic: a review and comparison of larvae from the northern Gulf of Mexico off Louisiana and Atlantic Coast of the U.S. *Bulletin of Marine Science* 44:1083-1105.

ESSIG, R.J. and C.F. COLE. 1986. Methods of estimating larval mortality from daily increments in otoliths. *Transactions of the American Fisheries Society*. 115:34-40.

FUKUHARA, O. and K. KUNIYUKI. 1978. Morphological development in the wild larvae of Madai, *Chrysophrys major*, as compared to that in the laboratory reared larvae. *Bulletin of the Nansei Regional Fisheries Research Laboratory*. 11:19-25.

GINSBURG, I. 1929. Review of the weakfishes (*Cynoscion*) of the Atlantic and Gulf coasts of the United States, with a description of a new species. *Bulletin of the Bureau of Fisheries*. 65:71-85.

GOVONI, J.J., A.J. CHESTER, D.E. HOSS and P.B. ORTNER. 1985. An observation of episodic feeding and growth of larval *Leiostomus xanthurus* in the northern Gulf of Mexico. *Journal of Plankton Research.* 7:137-146.

GUNTER, G. 1945. Studies on marine fishes of Texas. *Publications of the Institute of Marine Science.* 1:1-190.

GUTHERZ, E.J., G.M. RUSSELL, A.F. SERRA and B.A. ROHR. 1975. Synopsis of the northern Gulf of Mexico industrial and foodfish industries. *Marine Fisheries Review.* 1:1-11.

HERKE, W.H., B.D. ROGERS, and J.A. GRIMES. 1984. The study of the seasonal presence, relative abundance, movements, and use of habitat types of estuarine-dependent fishes and economically important decapod crustaceans on the Sabine National Wildlife Refuge. (Final Report) Louisiana Cooperative Fisheries Research Unit, Louisiana State University, Baton Rouge, 3 Vol. 933 p.

HEWITT, R.P., G.H. THEILACKER and N.C.H. LO. 1985. Causes of mortality in young jack mackerel. *Marine Ecology - Progress Series.* 26:1-10.

HILDEBRAND, H.H. 1955. A study of the fauna of the pink shrimp *(Penaeus duorarum* Burkenroad) grounds in the Gulf of Campeche. *Publications of the Institute of Marine Science.* 4:169-232.

HOUDE, E.D. and L.J. SWANSON, Jr. 1975. Description of eggs and larvae of yellowfin menhaden, *Brevoortia smithi. Fishery Bulletin.* 73:660-673.

KENDALL, A.W., JR., E.H. AHLSTROM and H.G. MOSER. 1984. Early life history stages of fishes and their characters. p. 11-22. In *Ontogeny and Systematics of Fishes.* Special Publication 1, American Society of Ichthyologists and Herpetologists.

MOSHIN, A.K. MOHAMMAD. 1973. Comparative osteology of the weakfishes (Cynoscion) of the Atlantic and Gulf coasts of the United States (Pisces-Sciaenidae). Ph.D. Thesis, Texas A&M University, College Station. 148 p.

NAKAMURA, E.L. 1981. Sciaenid resources in the Gulf of Mexico. p. 29-39. In H. Clepper (ed) Marine Recreational Fisheries. Vol. 6, Proceedings 6th Annual Recreational Fisheries Symposium, Houston, Texas. Prepared for the Sport Fishing Institute, Washington, D.C. 212 p.

O'CONNELL, C.P. 1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. *Fishery Bulletin.* 78:475-489.

PASCHALL, R.L. 1986. Biochemical systematics of the seatrouts of the western Atlantic genus *Cynoscion.* M.S. Thesis, University of New Orleans, Louisiana. 100 p.

PETERS, D.S., J.C. DEVANE, Jr., M.T. BOYD, L.C. CLEMENTS and A.B. POWELL. 1978. Preliminary observations of feeding, growth and energy budget of larval spot (*Leiostomus xanthurus*). Annual Report NMFS, Beaufort Laboratory, Beaufort, NC. 1978:377-394.

PETERS, K.M. and R.H. McMICHAEL, Jr. 1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. *Estuaries.* 10(1):92-107.

ROESSLER, M.A. 1970. Checklist of fishes in Buttonwood Canal, Everglades National Park, Florida, and observations on the seasonal occurrence and life history of selected species. *Bulletin of Marine Science of the Gulf and Caribbean.* 20:860-893.

ROITHMAYR, C.M. 1965. Review of the industrial bottomfish fishery in the northern Gulf of Mexico, 1959-1962. U.S. Fish and Wildlife Service. *Commercial Fisheries Review.* 27:1-6.

SHLOSSMAN, P.A. and M.E. CHITTENDEN, Jr. 1981. Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius. Fishery Bulletin.* 79:649-669.

STENDER, B.W. 1980. Descriptions, illustrations, and distribution of the early life history stages of *Cynoscion nothus*, with notes on related species. M.S. Thesis, College of Charleston, Charleston, SC. 55 p.

TANIGUCHI, A.K. 1979. Survival and growth of larval spotted seatrout (*Cynoscion nebulosus*) larvae in relation to temperature, prey abundance and stocking densities. International Council for the Exploration of the Sea, ICES/ELH Symp./RA:1. 24 p.

TAUBERT, B.D. and D.W. COBLE. 1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica. Journal of the Fisheries Research Board of Canada.* 34:332-340.

THEILACKER, G.H. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. *Fishery Bulletin.* 76:403-414.

———————. 1986. Starvation induced mortality of young sea caught jack mackerel, *Trachurus symmetricus* determined with histological and morphological methods. *Fishery Bulletin.* 84:1-17.

UNIVERSITY OF TEXAS. 1984. Mariculture Program Report, 1982-1983. 36 p.

WARLEN, S.M. 1981. Age and growth of larvae and spawning time of Atlantic croaker in North Carolina. *Proceedings of the Annual Conference of the Southeast Association of Game and Fish Commissioners.* 34:204-214.

——————— and A.J. CHESTER. 1985. Age, growth, and distribution of larval spot, *Leiostomus xanthurus,* off North Carolina. *Fishery Bulletin.* 83:587-599.

WEINSTEIN, M.P. and R.W. YERGER. 1976. Protein taxonomy of the Gulf of Mexico and Atlantic Ocean seatrouts, genus *Cynoscion. Fishery Bulletin.* 74:599-607.

YIN, M.C. and J.H.S. BLAXTER. 1986. Morphological changes during growth and starvation of larval cod (*Gadus morhua* L.) and flounder (*Platichthys flesus* L.). *Journal of Experimental Marine Biology and Ecology.* 104:215-228.

Contributions in Marine Science. (1989) Vol. 31:51–59.

REDESCRIPTION OF LARVAE OF THE PINFISH, *LAGODON RHOMBOIDES* (LINNAEUS) (PISCES, SPARIDAE)

Glen G. Zieske

Louisiana Department of Wildlife and Fisheries
P.O. Box 98000
Baton Rouge, Louisiana 70898-9000

ABSTRACT

Larvae of the pinfish, *Lagodon rhomboides* (Linnaeus), were collected in the Northern Gulf of Mexico off the central coast of Louisiana. Morphometric, meristic and pigmentation characters of fifty-five larvae, ranging from 3.4 to 14.0 mm standard length (SL), are discussed. Fin ray development begins at 4.3 mm SL and is complete by 12.7 mm SL. The juvenile stage is fully reached by 13.9 mm SL, at which time pigmentation resembles that of the adult and fin ray development is complete.

INTRODUCTION

Adult pinfish, *Lagodon rhomboides*, range from Cape Cod and Bermuda to Yucatan, including the Gulf of Mexico and the Bahamas (Caldwell 1957; Yocum 1971). Presently there are no recreational or commercial fisheries for the pinfish in the Gulf, probably due to the species' small size. Spawning takes place offshore, probably near the surface (Hildebrand and Cable 1938; Caldwell 1957; Springer 1957; Cameron 1969; Hansen 1970) in Atlantic coast waters. There is no literature on spawning area in the Gulf of Mexico, however larval pinfish are found inshore between the months of October and April (Ditty 1986; Ditty and Zieske, in review).

Larval development of the pinfish was first described by Hildebrand and Cable (1938) from larvae collected near Beaufort, N.C. Although this description was based on specimens from 5.0 to 40.0 mm long, overall sample size was small for the smaller larvae, with a lack of specimens over much of the size range.

The current study includes larvae less than 5.0 mm SL, and describes distinctive pigment patterns not reported by previous workers.

Specimens examined were collected by the Louisiana Department of Wildlife and Fisheries for the Louisiana Offshore Oil Port (LOOP), off the central coast of Louisiana. Additional specimens were obtained from the Oregon II cruises of 1983 for the South East Area Marine Assessment Program (SEAMAP) in the Northern Gulf of Mexico.

MATERIALS AND METHODS

Larvae from the LOOP project (Fig. 1) were collected from November 1982 to April 1984 with a 60 cm diameter BNF-opening/closing type frame, equipped with 363 micron mesh nets. Larvae from the SEAMAP project were collected using a 60 cm diameter MARMAP bongo frame equipped with 333 micron mesh nets. Upon collection, plankton samples were fixed in 10% formalin and later preserved in 70% ethanol until fish larvae could be removed and examined. LOOP specimens were deposited at the Louisiana Department of Wildlife and Fisheries, Baton Rouge office, while SEAMAP larvae were on loan from the SEAMAP archive center, Bureau of Marine Research, Florida Department of Natural Resources, St. Petersburg, Florida.

Larvae of *Lagodon rhomboides* were examined under a microscope equipped with an ocular micrometer. Fifty-five larvae, ranging from 3.4 to 13.9 mm SL, were examined. Data were grouped for fish within each developmental size class (pre-flexion, flexion, post-flexion and juvenile) and measurements were converted into percentages of SL. All measurements and fin ray counts were made on the left side of the fish.

At least 10 specimens from each size class were examined, with one specimen from each range being stained with alizarin (Brubaker and Angus 1984) for drawing and fin ray count purposes. The following measurements were made:

Standard length (SL) - symphysis of upper jaw to tip of notochord (preflexion larvae) or posterior edge of hypurals (flexion and post-flexion larvae).

Predorsal length (PDL) - symphysis of upper jaw to dorsal origin.

Preanal length (PAnL) - symphysis of upper jaw to anal origin.

Prepelvic length (PPvL) - symphysis of upper jaw to base of pelvic fin.

Snout length (SnL) - symphysis of upper jaw to anterior margin of eye.

Head length (HL) - symphysis of upper jaw to posterior edge of operculum.

Orbit diameter (OD) - horizontal diameter of orbit.

Maxillary length (MxL) - length of maxillary bone as measured on edge of greatest length.

Anus/anal fin gap (Gap) - posterior margin of anus to first anal fin element base.

Body depth at cleithrum (BDc) - vertical distance between dorsal body margin and ventral symphysis of cleithrum.

Body depth at anus (BDa) - vertical distance between dorsal body margin and ventral tip of anus.

DESCRIPTION OF LARVAE

Identification

The specimens used in this description were identified as *Lagodon rhomboides* by comparing pigment patterns, myomere counts, fin development and overall appearance with larvae described by Hildebrand and Cable (1938).

Morphometry and Pigmentation

Table 1 summarizes morphometric values of the specimens of *Lagodon rhomboides* in percentage of SL. Larvae are grouped in preflexion, flexion, postflexion and juvenile stages. Pigmentation patterns are described for preflexion (3.4 - 4.9 mm SL), flexion (5.0 - 7.9 mm SL) and postflexion (8.0 11.9 mm SL) larvae, and juveniles (12.0 - 13.9 mm SL), specimens ranging from 12.0 to 12.9 mm SL are considered early juveniles due to completion of fin ray development (Table 2).

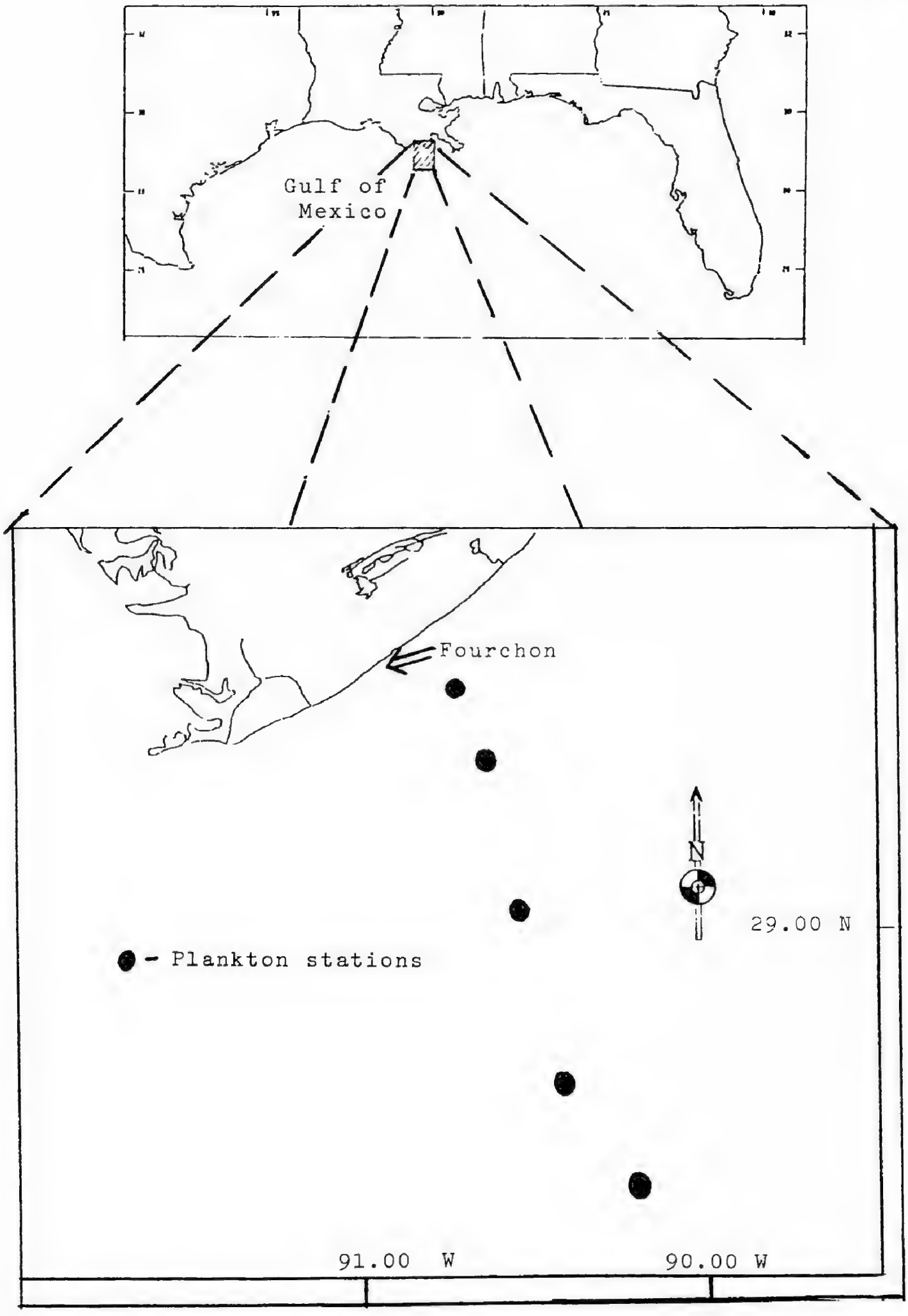


FIG. 1. Study area off the coast of Louisiana.

TABLE 1

Summary of morphometrics of larval *Lagodon rhomboides* given in percentage of SL, (mean, standard deviation and range).

	Pre-flexion (3.4-4.9 mm) n = 10	**Flexion (5.0-7.9 mm) n = 15**	**Post-flexion (8.0-11.9 mm) n = 20**	**Juvenile (12.0-13.9 mm) n = 10**
PDL	-	37.78 ± 1.78 35.20-40.00	32.31 ± 0.36 31.90-32.90	32.80 ± 0.52 31.90-33.20
PAnL	-	54.21 ± 0.50 53.40-55.00	52.44 ± 0.52 51.90-53.20	52.02 ± 0.66 50.90-52.60
PPvL	-	-	31.34 ± 0.70 30.30-32.10	33.12 ± 0.19 32.90-33.40
SnL	4.67 ± 0.59 4.00-5.80	7.09 ± 0.55 6.10-8.00	7.04 ± 0.31 6.70-7.50	7.94 ± 0.17 6.80-8.20
HL	22.02 ± 0.60 21.30-23-00	26.82 ± 0.68 25.80-27.90	23.40 ± 0.82 22.40-24.50	24.16 ± 0.11 24.00-24.30
OD	9.28 ± 0.91 8.10-10.60	10.59 ± 0.24 10.20-11.00	8.99 ± 0.45 8.30-9.70	9.26 ± 0.36 8.90-9.80
MxL	4.11 ± 4.34 0.00-8.70	10.68 ± 0.18 10.50-11.00	9.76 ± 0.34 9.20-10.10	8.80 ± 0.25 8.50-9.10
GAP	-	8.00 ± 1.64 5.90-10.00	2.19 ± 1.90 0.00-4.50	-
BDc	20.12 ± 1.32 18.20-22.40	23.12 ± 0.12 22.90-23.30	22.49 ± 0.41 21.90-23.00	22.34 ± 0.22 22.00-22.60
BDa	16.34 ± 1.85 13.20-19.60	18.08 ± 0.18 17.80-18.40	19.64 ± 1.36 18.00-21.10	21.82 ± 1.04 20.90-23.40

Preflexion Larvae (Fig. 2-A,B)

The smallest larva available for examination measures 3.4 mm SL. One melanophore is present on the nape. The only pigment is in the dorsal midline

TABLE 2

Summary of fin development sequence in larvae of *Lagodon rhomboides*; measurements given in mm SL.

Fin	Buds Appear	Rays Appear	Full Complement of Rays
Dorsal		5.4	10.5
Anal		5.4	10.5
Caudal			
Principal		4.3	11.6
Secondary		5.7	12.2
Pelvic	8.4	10.5	12.7
Pectoral	3.3	4.3	12.2

of this larva. Pigment in the ventral midline is characteristic, with one melanophore just anterior to the cleithral symphysis, another on the isthmus and a third in the vent area (Hildebrand and Cable 1938). There is a series of 8 - 12 melanophores along the ventral midline from the origin of the anal finfold to the base of the caudal fin. The dorsal surface of the visceral mass and the posterior surface of the anus are both heavily pigmented. One melanophore is present ventral to the otic capsule of the developing hind-brain. By 4.9 mm SL a small melanophore is present on top of the head. In specimens under 4.0 mm SL, a finfold extends from the top of the head to the visceral mass, interrupted only by the anus. Principal caudal rays and pectoral rays start to develop by 4.3 mm SL.

Flexion Larvae (Fig. 2-C)

Larvae between 5.0 and 7.9 mm SL undergo flexion and some new pigmentation starts to develop. By 5.9 mm SL 2 - 4 punctate melanophores are present at the base of the developing caudal fin rays. Two or three melanophores occur dorsally on the caudal peduncle. Also present are 2 - 4 melanophores internally over the notochord between the middle of the dorsal finfold and base of the caudal fin. As larvae reach 6.9 mm SL the nape melanophore becomes imbedded in the nape musculature, and the internal melanophores over the notochord are more visible. Larvae 7.0 - 7.9 mm SL are completing flexion and show no great change in pigmentation patterns. There can be up to six melanophores present on the dorsal surface of caudal peduncle, and pigment at the base of the caudal fin rays tends to be more stellate than punctate in these larvae. A remnant of the finfold can be seen in the anus - anal fin gap of larvae 5.4 - 7.8 mm SL. Dorsal and anal fin rays begin to develop by 5.4 mm SL, and by 5.7 mm SL the secondary caudal fin rays are apparent.

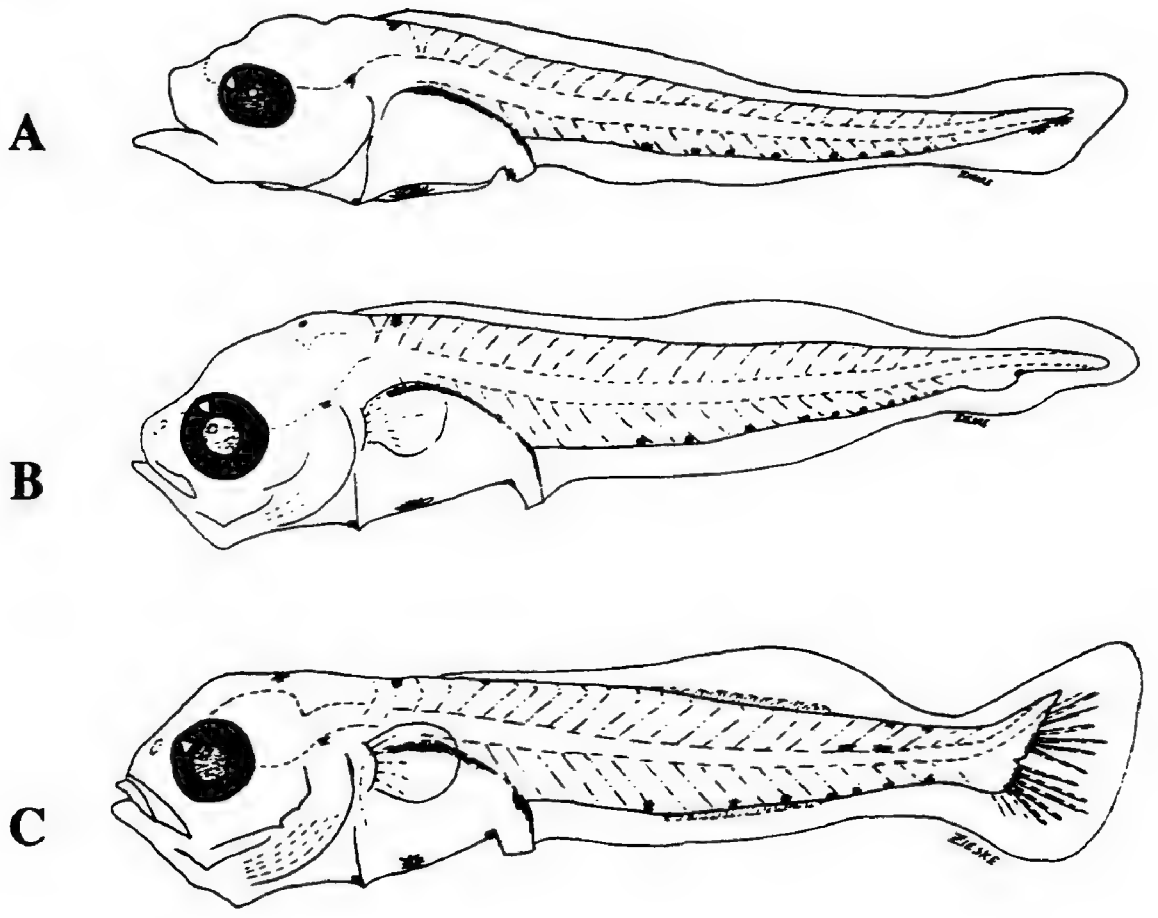


FIG. 2. Developmental series of *Lagodon rhomboides*: (pre-flexion) A-3.4 mm B-4.5 mm; (flexion) C-5.2 mm; (post-flexion) D-8.4 mm E-10.8 mm; (juvenile) F-13.8 mm.

Postflexion Larvae (Fig. 2-D,E)

Larvae 8.0 - 11.9 mm SL have completed flexion. By 8.9 mm SL the head pigmentation is more dense, and the melanophore under the otic capsule is embedded and difficult to see, but can be viewed by rolling the larva onto its dorsum and looking down through either gill opening. Characteristic ventral midline pigment described in preflexion larvae is still present. The pigment on the dorsal surface of the visceral mass is less dense than in younger larvae. Nape pigment has moved deeper into the musculature, and the melanophores on the dorsal surface of the caudal peduncle are still present. The melanophore at the nape can no longer be seen in larvae greater than 9.5 mm SL, and larvae larger than 9.6 mm SL show slight dorso- and ventro-lateral scattering of pigment. By 10.9 mm SL larvae are more dorso- and ventro-laterally pigmented; head pigment starts to spread anteriorly onto the snout and is more dense than in smaller larvae. The vertical bands of pigment characteristic in the juvenile of this species begin to form in larvae 11.0 - 11.9 mm SL, however the pigment observed in the younger larvae is also present. Four of five larvae in this size range possess 1 - 3 melanophores under the outer edge of the preoperculum. The internal melanophores over the notochord are still visible but may be slightly obscured by the vertical band pigmentation. Head pigmentation continues to spread anteriorly onto the snout. By 10.5 mm SL development of dorsal and anal fins is complete, and by 11.6 mm SL the principal caudal rays have completed development.

Juveniles (Fig. 2-F)

Specimens 12.0 - 13.9 mm SL are considered early juveniles due to completion of fin formation. All of these specimens had 1 - 3 melanophores under the outer edge of the preoperculum. Vertical band formation continues and is complete by 13.6 mm SL. By 13.4 mm SL the snout is densely pigmented. Characteristic pigmentation of juveniles consists of:

seven vertical bars on the sides of the body,
ventral midline pigmentation as mentioned for younger larvae,
internal melanophores over the notochord and
one melanophore below the otic capsule.

By 12.7 mm SL all fin formation is complete and the full adult complement is present for each fin.

COMPARISON WITH OTHER LARVAE

Larval sparids are often confused with the larvae of other families of fishes, most frequently the haemulids, gerreids and sciaenids (Fig. 3). Sparids can easily be distinguished from haemulids by myomere count; 24 in sparids and 26 - 27 in haemulids (Watson 1983). Sparids are also easily distinguished from gerreids (at sizes larger than 4.5 mm SL), by the presence in gerreids of an extremely protrusible under jaw with a premaxillary spine that extends up a

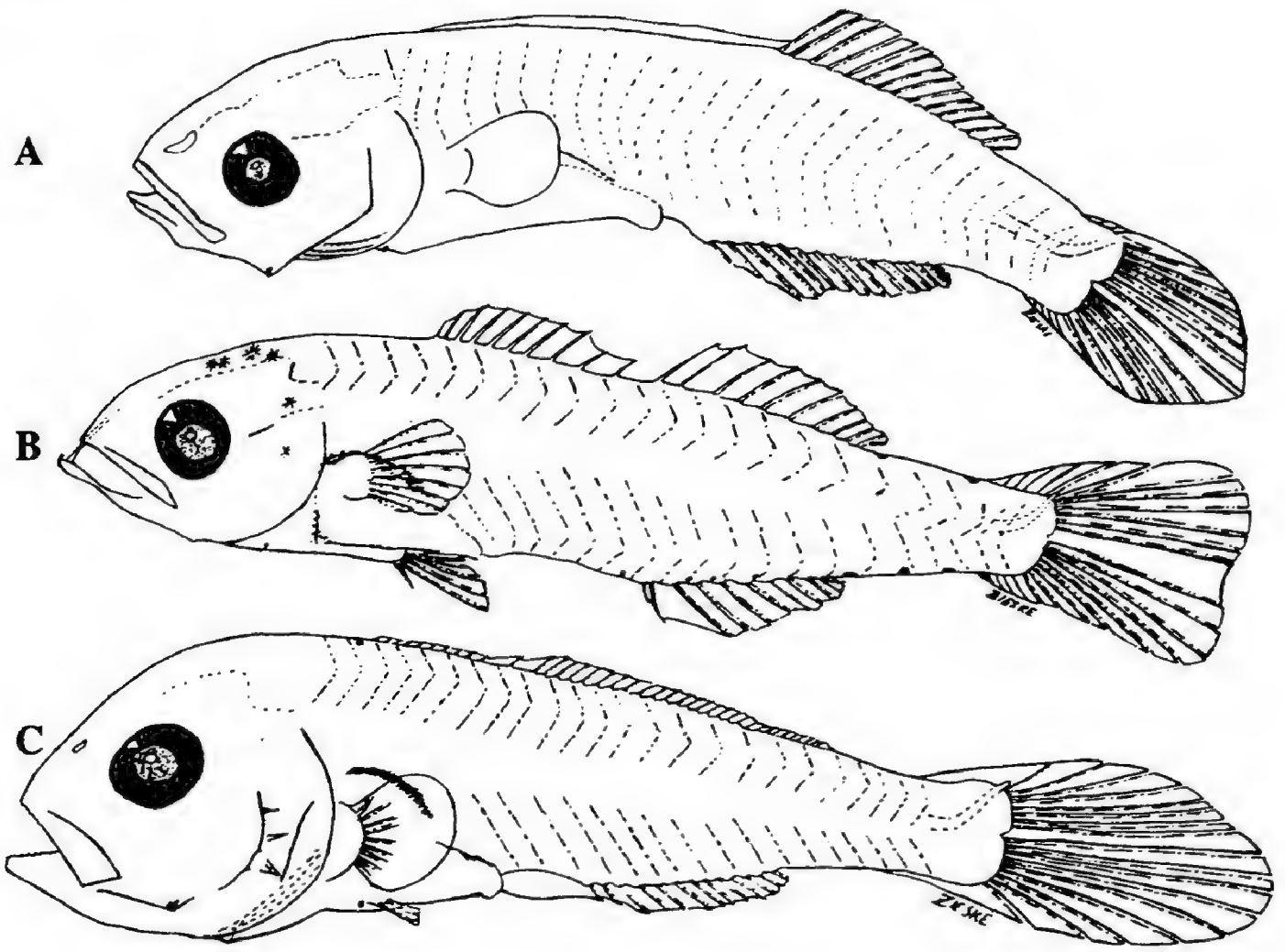


FIG. 3. Larvae of families commonly confused with sparids.
A: Haemulidae (7.5 mm)
B: Gerreidae (10.0 mm)
C: Sciaenidae (7.4 mm).

groove between the eyes. Sparids differ from sciaenid larvae by the presence in sciaenids of longer anus-anal fin gap and a melanophore at the angle of the lower jaw (Powles and Stender 1978). Furthermore, in northern Gulf of Mexico specimens the dorsal fin base is longer than the anal fin base in larval sciaenids, but are approximately equal in length in larval sparids.

Other sparids that are frequently collected in the northern Gulf of Mexico are *Diplodus holbrooki, Archosargus probatocephalus, Stenotomus caprinus* and *Calamus* spp.

Larvae of *D. holbrooki* have not been described. Juveniles of *D. holbrooki* have five vertical bars on the sides of the body (Hildebrand and Schroeder 1928), whereas at comparable sizes or stages of development, larvae of *L. rhomboides* have seven.

Ten specimens of *A. probatocephalus* were examined for comparison with *L. rhomboides*. Juveniles of both species exhibit similar pigmentation patterns with seven vertical bars on the sides of the body, but they are readily discernible from each other during larval stages by differences in ventral midline pigmentation.

A. probatocephalus larvae lack the ventral melanophore series described here for *L. rhomboides*, and have only two melanophores on the anal fin base. These data agree with those of Hildebrand and Cable (1938).

Larvae of *S. caprinus* and *Calamus* spp. are poorly known, therefore comparisons with larval *L. rhomboides* are not possible at this time.

ACKNOWLEDGMENTS

I would like to thank the Louisiana Department of Wildlife and Fisheries as well as LOOP Inc. for the use of specimens collected during their ongoing project and SEAMAP for loan of any sparids they had on archive. Thanks go to Jim Ditty, L.S.U. Center for Wetland Resources, and Harry Blanchet, Louisiana Department of Wildlife and Fisheries, as well as all my co-workers for their critical reviews of this manuscript. This effort is dedicated to the memory of my grandmother, Queen E. Zieske.

LITERATURE CITED

BRUBAKER, J.M. and R.A. ANGUS. 1984. A procedure for staining fish with alizarin without causing exfoliation of scales. *Copeia*. **1984(4)**:989-990.

CALDWELL, D.K. 1957. The biology and systematics of the pinfish, *Lagodon rhomboides* (Linnaeus). *Bulletin of the Florida State Museum*. **2(6)**:77-173.

CAMERON, J.N. 1969. Growth, respiratory, metabolism and seasonal distribution of juvenile pinfish (*Lagodon rhomboides* Linnaeus) in Redfish Bay, Texas. *Contributions in Marine Science*. **14**:19-36.

DITTY, J.G. 1986. Ichthyoplankton in neritic waters of the Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality. *Fishery Bulletin, U.S.* **84(4)**:935-946.

_____, G.G. ZIESKE, and R.F. SHAW. In Review. Seasonality and depth distribution of larval fishes in the northern Gulf of Mexico above 26°00′ N latitude.

HANSEN, D.J. 1970. Food, growth, migration, reproduction and abundance of pinfish, *Lagodon rhomboides* and Atlantic croaker, *Micropogon undulatus*, near Pensacola, Florida. *Fishery Bulletin, U.S.* **68(1)**:135-146.

HILDEBRAND, S.F. and L.E. CABLE. 1938. Further notes on the development and life history of some teleosts at Beaufort, N.C. *Bulletin of the U.S. Bureau of Fisheries*. **48(24)**:505-641.

_____ and W.C. SCHROEDER. 1928. Fishes of Chesapeake Bay. *Bulletin of the U.S. Bureau of Fisheries*. **43(part 1)**:1-366.

POWLES, H. and B.W. STENDER. 1978. Taxonomic data on the early life history stages of Sciaenidae of South Atlantic Bight of the United States. South Carolina Marine Resources Center, Technical Report Series. No. 31. 64 p.

SPRINGER, S. 1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. *Ecology*. **38(1)**:166-177.

WATSON, W. 1983. Redescription of larvae of the pigfish, *Orthopristis chrysoptera* Linnaeus (Pisces, Haemulidae). *Fishery Bulletin, U.S.* **81(4)**:847-854.

YOCUM, T.G. 1971. Pinfish and rockcut goby, fishes new to the Bahamas. *Quarterly Journal of the Florida Academy of Science*. **34(2)**:131.

Contributions in Marine Science. (1989) Vol. 31:61–75.

EXPLOITED AND UNEXPLOITED HARD CLAM, *MERCENARIA MERCENARIA* (L.), POPULATIONS IN COASTAL GEORGIA

Randal L. Walker

Marine Extension Service
University of Georgia
P. 0. Box 13687
Savannah, Georgia 31416-0687

ABSTRACT

The growth rate, density, age structure, size structure and commercial size structure of 40 populations of the hard clam, *Mercenaria mercenaria* (L.) in the coastal waters of Georgia are described. The hard clam grows to a commercial size in 2 to 3 years throughout the coastal area of Georgia, excepting under extreme environmental conditions. Mean clam densities up to 151 clams m^{-2} occurred, with an overall mean density of 22 clams m^{-2} for the 40 populations. In non-fished or unexploited clam populations, a wide range of clam sizes (up to 11.8 cm in shell length) and clam ages (up to 40 years) may occur; however, the range of clam sizes and ages is narrowed in the presence of light or heavy fishing pressures. The range decreases with increases in fishing pressure.

INTRODUCTION

The hard clam, *Mercenaria mercenaria* (L.), fishery in the State of Georgia dates back to 1880 with peak landings of clams occurring in 1908 (Walker 1984a). Since 1932 and prior to 1981, clam landings have occurred in only 5 years in Georgia. With the increase in demands for clams by consumers and the decline in clam landings in traditional northern U.S. clamming areas due to pollution and overharvesting (National Marine Fisheries Service 1977), interest in clamming in Georgia has steadily increased among local as well as out-of-state fishermen. This coupled with the potential for mariculture of this species (Walker 1983; Walker 1984a,b) has led to a re-emergence of the fishery in Georgia with low but steadily increasing landings reported since 1981.

At present, the majority of the clam populations in Georgia represent natural unexploited populations. With time and increases in fishing pressures, these populations will undergo dramatic changes in population dynamics. Thus at this time, it would be useful to obtain baseline studies on undisturbed clam populations as well as on those already disturbed by fishing for future comparisons.

The purpose of this study was to assess the status of clam populations in the coastal waters of Georgia. This report describes distribution, densities, growth rates, population age structure, population size structure and commercial size structure for unharvested versus harvested clam populations in the coastal waters of Georgia.

METHODOLOGY

Clams were collected from 40 populations of coastal Georgia (13 from Wassaw Sound, 15 from Harris Neck, 1 from Crooked River, 1 from Cumberland Island, 7 from Christmas Creek and 3 from Ossabaw Island) by taking three 0.44 m^2 quadrat samples per site. A 66 × 66 cm square PVC frame was thrown on to the creek bottom and clams were dug by hand to a depth of 6 cm, placed in field sampling bags and marked as to locality. Clams were returned to the laboratory, where they were counted, measured for shell length (longest possible measurement, *i.e.*, anterior-posterior), and aged by shell sectioning techniques (see Rhoads and Lutz 1980; Rhoads and Pannella 1970). Growth curves for each clam were determined by measuring shell length at each summer annual ring increment.

Clams at each station were categorized according to the following commercial size groups: juveniles, <38 mm; pre-legal littlenecks, 38 to 44.4 mm; littlenecks, 44.4 to 67.0 mm; cherrystones, 68 to 77 mm; and chowders >78 mm in shell lengths. This classification scheme is similar to Godwin's (1967) scheme except that his littleneck size class (38 to 68 mm) was divided into prelegal littlenecks, those <44.4 mm and legal littlenecks, those >44.4 mm (Walker 1984a).

The criteria for classifying harvested and non-harvested populations is somewhat arbitrary. Nonharvested populations occur either in areas closed to the taking of shellfish or in opened areas where harvesting is not known to have occurred (both by personal observations and by talking with the six clammers in Georgia). Lightly harvested populations are those which fishermen have been observed or have reported working. Heavily fished populations are those in which clammers have been observed harvesting numerous times per year as well as over several years.

Recruitment is defined, in this study, as clams that survived the first year, *i.e.*, successful recruitment. Hard clams have a rapid growth rate in Georgia and after one year of growth, most predators are unable to prey upon them. Actual recruitment (*i.e.*, the total number of clam spat that settled per year) is unknown, as well as mortality rates.

RESULTS

The annual mean growth measurements of the various clam populations are given in Table 1. In 95% of populations sampled, clams reach a mean marketable size (44.4 mm in shell length or 25.4 mm in shell width) in 2 to 3 years; while, individual clams obtain this size in from under 2 to 7 years. The exceptions to this are Sapelo Sound Station 9 and Cumberland Island Station 1 in which 5 and 4 years of growth were required before commercial size was obtained, respectively.

An example of population shell size and age structure is given in Figure 1. Clams were aged up to a maximum of 40 years with an overall mean age of 10.8 years. In terms of shell length, the largest clam found was sized to 11.83 cm with an overall (N = 40 populations) mean shell length of 7.21 cm ± 1.12 cm S.D. Overall, clams less than 10 years old accounted for 60% of the harvested animals; whereas, clams 11 to 20, 21 to 30 and those greater than 30 years old accounted for 25%, 13% and 2% respectively (Fig. 2). As clam popu-

TABLE 1

Mean shell length in mm of hard clams, *Mercenaria mercenaria*, per annual band for each population.

Annual Baud	1	2	3	4	5	6	7	8	9	10
Wassaw Sound Population										
1	29.7	41.8	46.3	55.3	58.9	62.3	62.6	65.2		
2	22.0	38.2	50.4	58.8	64.8	70.5	75.2	70.5		
3	25.0	42.5	57.3	67.1	72.7	76.9	80.7	83.8	85.7	88.2
4	25.1	42.9	56.4	65.7	70.7	73.9	74.2	76.8	82.1	79.8
5	22.8	41.1	53.9	62.0	65.6	68.2	71.6	74.1	74.3	75.6
6	25.5	36.2	46.1	50.9	56.1	61.3	66.0	68.1	68.7	69.8
7	23.4	39.4	49.6	57.1	67.2	64.4	67.2	73.3		
8	24.3	39.9	53.2	60.0	64.3	67.1	63.2	70.4	71.4	72.6
9	23.9	42.0	57.2	65.7	70.5	74.0	76.3	77.2	79.0	79.9
10	21.3	70.2	53.4	61.0	65.1	67.0	69.8	71.7	73.2	73.1
11	21.5	41.3	55.3	64.0	69.9	73.7	76.8	79.7	83.6	85.9
12	24.3	42.1	57.3	66.1	71.6	75.4	78.6	79.5	80.8	83.0
13	25.8	43.2	56.5	64.8	70.1	73.9	78.3	79.1	81.7	81.6
St. Catherine's Sound										
1	21.2	36.1	48.7	54.7	61.1	65.6	70.5	72.6	75.4	73.0
2	23.9	40.0	53.0	61.6	67.0	70.7	73.6	74.8	75.0	77.9
3	23.0	36.9	52.5	60.8	67.5	73.4	77.1	78.7	81.6	83.8
Sapelo Sound										
1	27.0	42.1	52.7	60.6	65.0	65.1	66.9	68.4	69.8	71.1
2	21.1	41.7	53.8	62.0	69.0	72.1	75.7	76.0	78.3	80.4
3	23.2	38.9	53.3	61.2	66.5	70.2	73.7	76.1	78.3	78.7
4	25.5	37.2	48.6	56.8	62.5	66.2	68.1	70.8	72.9	74.3
5	24.7	39.8	53.4	60.7	66.2	66.4	68.4	70.1	71.9	74.7
6	25.6	41.6	54.9	61.8	66.4	69.4	72.3	73.1	74.8	76.0
7	25.5	39.6	49.1	55.3	59.6	62.8	64.7	66.2	67.1	68.6
8	29.0	46.9	57.8	61.7	65.0	68.4	69.1	70.0	69.3	70.6
9	16.8	26.9	35.9	42.1	46.6	50.1	50.4	52.5	53.1	54.0
10	26.2	44.9	53.0	59.1	59.1					
11	31.6	45.6	54.8	61.5	66.4	69.6	72.1	73.6	75.8	76.8
12	28.5	47.6	59.3	65.9	69.5	73.0	74.8	75.6	77.5	76.8
13	30.5	44.3	56.7	65.6	73.9	80.7	83.4	89.9	92.5	
14	25.9	41.4	52.3	59.3	64.1	67.7	70.9	72.2	73.7	74.9
15	33.0	47.2	56.5	62.8	67.2	70.4	72.6	74.7	76.6	80.8
Christmas Creek										
1	23.5	41.5	53.4	60.8	65.1	68.3	70.2	73.0	73.9	73.4
2	26.5	42.2	54.5	62.3	67.0	69.6	71.7	73.5	74.2	76.4
3	24.5	41.9	54.2	61.0	65.5	68.5	70.8	71.5	73.3	74.7
4	27.1	44.1	55.3	62.8	67.3	70.9	73.2	75.0	76.2	76.9
5	26.6	42.4	54.3	60.8	64.5	66.0	67.9	66.8	69.8	70.9
6	84.7	42.9	53.3	59.6	60.7	64.0	67.1	69.5	71.4	72.2
7	26.4	44.5	56.3	67.0	71.9	75.3	77.3	79.4	80.8	82.0
Cumberland Island										
1	16.5	26.0	38.3	47.3	53.5	56.8	59.7	62.0	62.0	64.8
Crooked River										
1	24.9	40.1	53.2	64.1	70.5	76.2	79.7	82.2	83.7	85.1

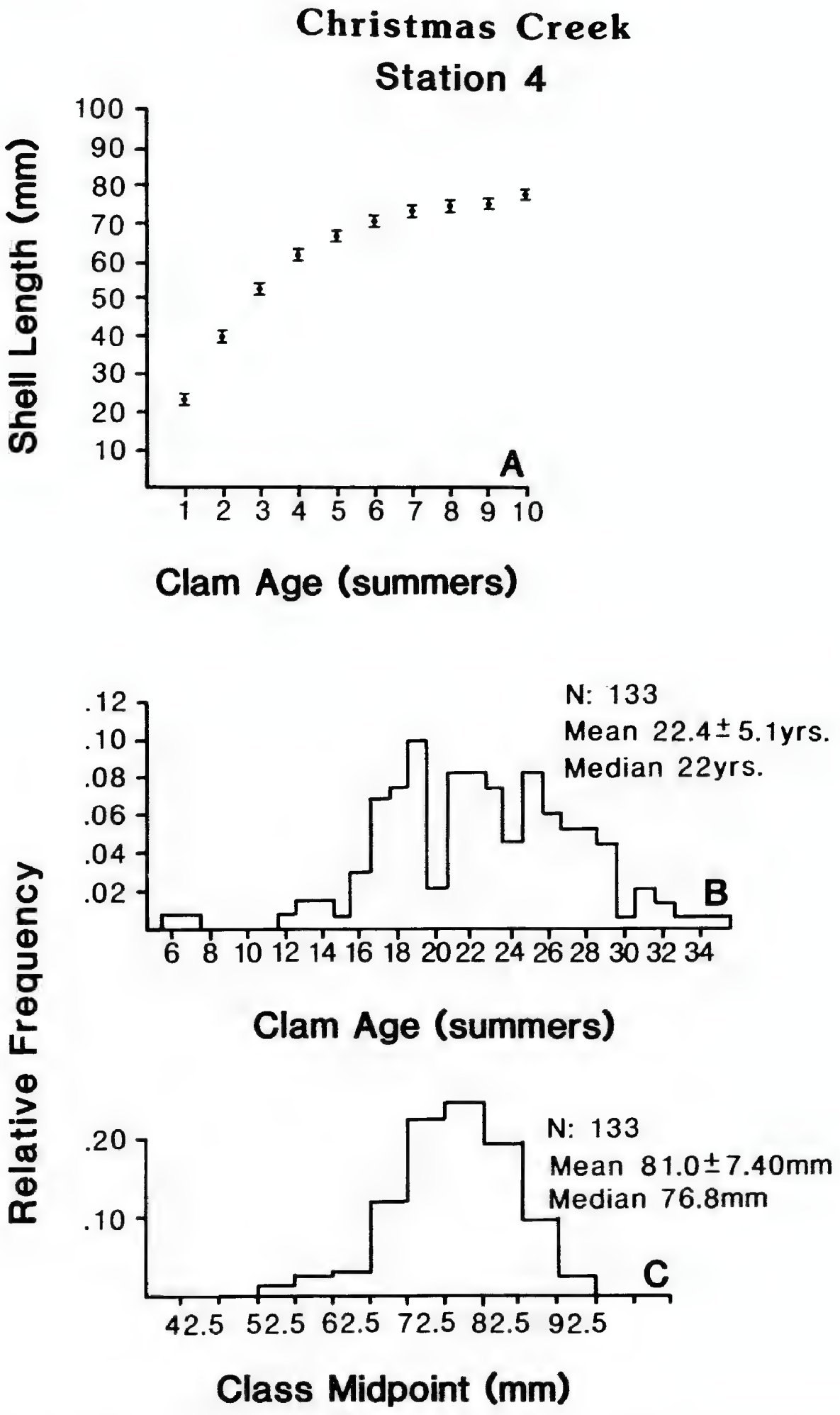


FIG. 1. Growth curve (a) (mean shell length ± one standard error), age, structure (b), and size structure of hard clam (c), *Mercenaria mercenaria* (L.), population 4 from Christmas Creek, Little Cumberland and Cumberland Islands, Georgia.

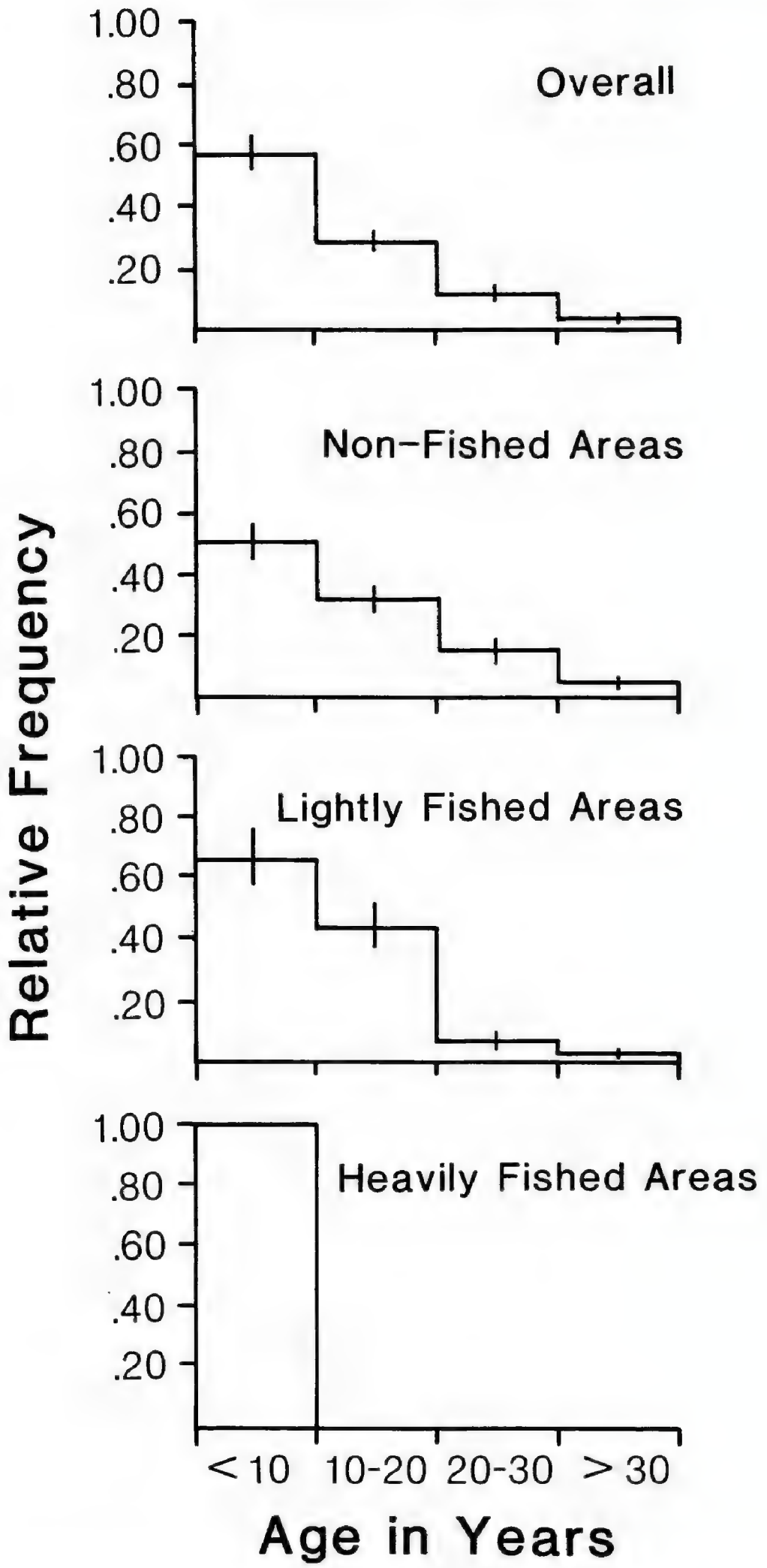


FIG. 2. Hard clam, *Mercenaria mercenaria* (L.), age structure in populations not fished, lightly fished, heavily fished, and overall data. Data are given as mean percent ± one standard error.

lations were fished, the percentage of older clams was reduced; whereas, the percentage of juveniles increased as fishing pressure increased (Fig. 2). Most populations appear to be growing populations as exhibited by the presence of successful recruiting individuals in the younger year classes. Christmas Creek Station 4 (Fig. 1) is the major exception in that in this dense population, only two individual clams were less than 10 years old. There has apparently been virtually no successful recruitment to this population in 12 years. Wassaw Sound Station 3 also had only 3 individuals less than ten years of age, with the majority of the clams being over 20 years of age.

In terms of commercial size grouping, juveniles accounted for 3% of the overall population (N = 40 populations) with pre-littlenecks, littlenecks, cherrystones and chowders accounting for 4%, 32%, 28% and 33% respectively (Fig. 3). Chowders dominated in numbers in 40% of the populations. Cherrystones and littlenecks dominated in numbers in 38% and 22% of the clam populations respectively. Decreasing fishing pressure seemed to decrease the relative abundance of larger size classes; chowders dominated in non-fished stations (N = 27) and percentages progressively decreased in areas

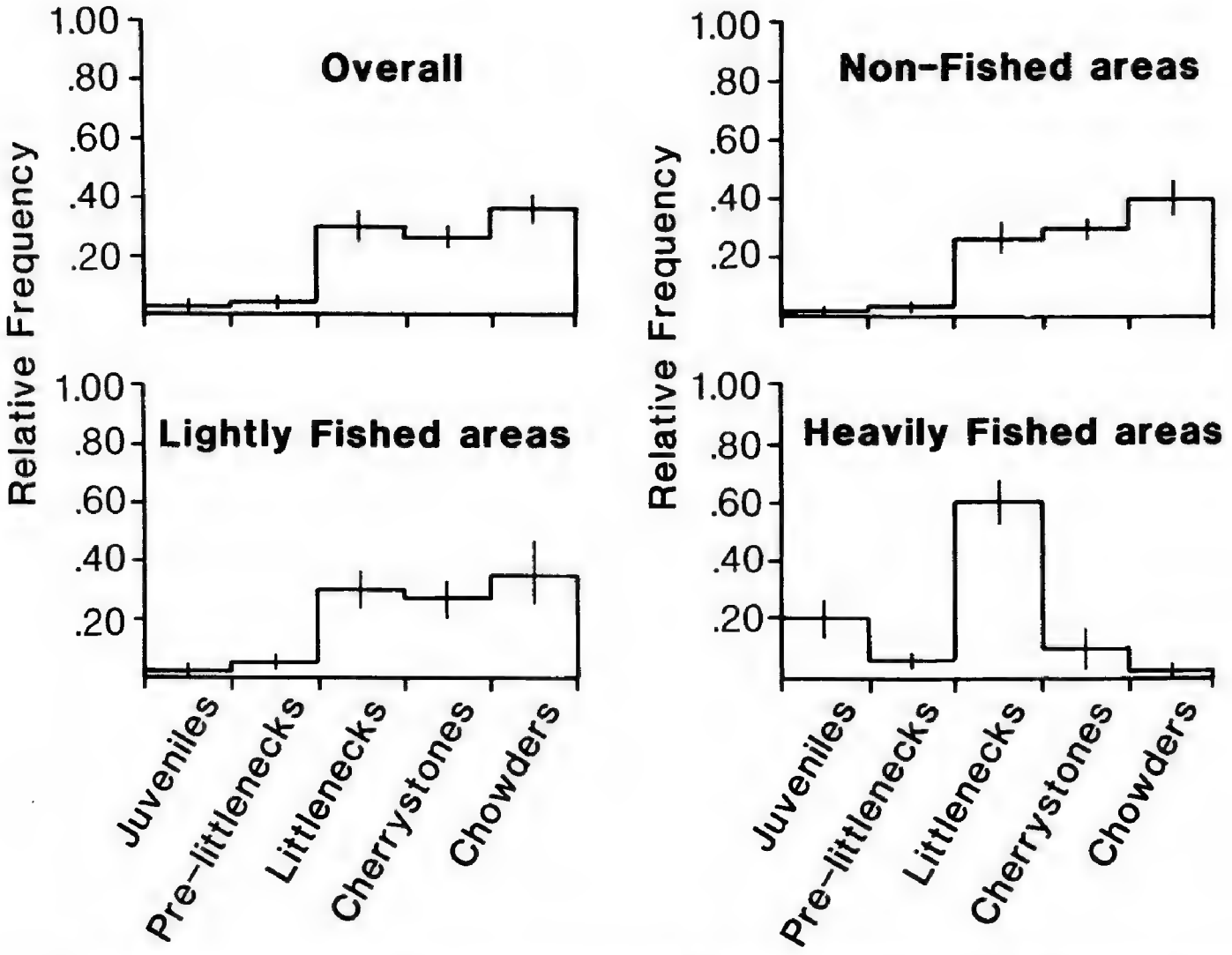


FIG. 3. Relative overall percentages of commercial grouping of hard clams, *Mercenaria mercenaria* (L.), from all populations sampled in coastal Georgia. Percentage of commercial groupings of clams in non-fished, lightly fished and heavily fished clam populations. Data are given as mean percent ± one standard error.

lightly fished (N = 11) and areas intensely fished (N = 2). The percentage of littlenecks increased with an increase in fishing pressure (Fig. 3).

Mean clam densities ranged from less than 1 to 151 clams per square meter (Table 2); whereas, individual samples ranged from 0 to 216 clams per square meter. Overall average density of the 40 clam populations sampled was 22 clams per square meter. Large differences in clam numbers per sample per station were observed. For instance, at Christmas Creek Station 5, the number of clams per sample was 95 from a shelly area and 4 and 14 from a more muddy area.

DISCUSSION

The results of this study show that the growth rate of the various clam populations in coastal Georgia result in a marketable product in 2 to 3 years. These rates agree with growth rates observed in other natural clam populations in Georgia (Walker 1984a, Quitmyer, Hale and Jones 1985; Walker and Stevens 1988). Furthermore, they agree with growth rates obtained from hatchery reared clam seed in Georgia (Walker 1984a,b), in South Carolina (Eldridge, Waltz, Gracy and Hunt 1976; Eldridge, Eversole and Whetstone 1979) and in Florida (Menzel 1964).

Of the 40 clam populations, only clams at Cumberland Island Station 1 and Sapelo Sound Station 9 required more than three years of growth to obtain a mean marketable size. At Sapelo Sound Station 9, clams occurred on top of an oyster reef well above the mean low water mark. Clams here occur in a dense substratum of dead oyster shell and are estimated to be uncovered from the tide for 6 hours per tidal cycle. At the Cumberland Island Station, clams occur in a substratum of sand and *Spartina alterniflora* short form roots. Clams here are estimated to be uncovered approximately 8 hours per tidal cycle (mean tidal amplitude in Georgia is 2.1 m, Johnson, Hillestad, Shanholtzer and Shanholtzer 1974). Clams at Cumberland Island Station 1 required 4 years versus 5 years at the Sapelo Sound Station to obtain commercial size. It may be that substratum (in this case, clams growing in dense shell substratum) and related current regime inhibits clam growth more than moderate increases in exposure time. For instance, in Sapelo Sound Stations 9 and 10, the two populations occur within 12 meters of each other. Stations 9 and 10 occur on the same oyster reef, but clams at Station 10 occur in a shelly mud substratum and are estimated to be exposed for 5.5 hours per tidal cycle. Yet clams at Station 10 grew almost twice as fast as those at Station 9 with only an 1/2 hour greater exposure time. Another example of this may be the clam populations in Beach Creek (St. Catherine's Stations 1 and 2). Both populations occurred within approximately 4 meters of each other. Clams at Station 1 occurred in a shelly-sand substratum at the mean low water mark; whereas, those at Station 2 occurred in mud up on the creek bank and are estimated to be uncovered for approximately 6 hours per tidal cycle. Yet clams at Station 2 have a higher mean size per year than those at Station 1. Thus it appears that substratum and the related current regime in certain cases may be more inhibitory to clam growth than exposure time.

TABLE 2

Habitat type, substratum type, mean density of clams, *Mercenaria mercenaria*, ± standard deviation per m^2, and relative commercial harvesting pressure per population.

Area/Station	Habitat Type	Substratum Type	Mean Density per m^2	Commercial Harvesting
Wassaw Sound				
1	Intertidal Flat	Shell/Sand	8.8 ± 7.7	Intense
2	Intertidal Flat	Shell/Sand	20.3 ± 8.9	Intense
3	Creek	Mud	13.5 ± 18.4	None
4	Feeder Creek	Shell/Mud	3.0 ± 1.5	None
5	Feeder Creek	Shell/Mud	47.3 ± 30.9	Light
6	Feeder Creek	Shell/Mud	<1	None
7	Feeder Creek	Shell/Mud	3.2 ± 4.5	None
8	Feeder Creek	Shell/Mud	18.0 ± 8.9	None
9	Feeder Creek	Shell/Mud	6.8 ± 4.1	None
10	Feeder Creek	Sand/Shell	36.0 ± 45.0	Light
11	Creek	Shell	14.0 ± 10.2	Light
12	Creek	Shell/Sand	10.0 ± 8.0	None
13	Creek	Shell/Mud	12.8 ± 15.2	None
St. Catherine's Sound				
1	Creek	Shell/Mud	10.1 ± 5.6	Light
2	Creek	Mud	11.5 ± 8.3	Light
3	Soumd - Intertidal Flat	Shell/Sand	2.1 ± 1.6	Light
Sapelo Sound				
1	Feeder Creek	Shell/Mud	4.0 ± 3.5	None
2	Creek	Shell/Mud	<1	Light
3	Creek	Shell/Mud	10.1 ± 5.7	Light
4	Creek	Shell/Mud	3.0 ± 1.4	None
5	Creek	Shell/Mud	23.0 ± 14.1	None
6	Feeder Creek	Shell/Mud	8.1 ± 6.7	None
7	Feeder Creek	Shell/Mud	7.0 ± 4.8	None
8	Feeder Creek	Shell/Mud	50.0 ± 21.3	None
9	Intertidal Flat	Shell	21.0 ± 8.9	None
10	Intertidal Flat	Shell/Mud	20.0 ± 16.1	None
11	Creek	Shell/Mud	46.6 ± 25.7	None
12	Feeder Creek	Shell/Mud	11.0 ± 10.8	None
13	Feeder Creek	Shell/Mud	6.1 ± 5.8	None
14	Creek	Shell/Mud	4.2 ± 2.6	Light
15	Creek	Shell/Mud	5.3 ± 3.3	Light
Crooked River				
1	River	Sand	<1	Light
Christmas Creek				
1	Feeder Creek	Shell/Mud	34.1 ± 19.6	None
2	Feeder Creek	Shell/Mud	6.1 ± 3.9	None
3	Feeder Creek	Shell	73.5 ± 27.2	None
4	Feeder Creek	Mud/Shell	151.0 ± 10.2	None
5	Feeder Creek	Shell to Mud*	85.7 ± 92.6	None
6	Feeder Creek	Shell/Mud	14.3 ± 7.7	None
7	Feeder Creek	Shell/Mud	67.7 ± 52.1	None
Cumberland Island				
1	Intertidal Flat	Sand/Grass	10 to 15**	None

* Creek bottom had only small area of shell; most of creek bottom was mud. High density of clams (95 per sample) occurred in shell bottom; whereas, 14 and 4 clams occurred per sample in mud.

** Estimated. These animals were collected while accompanying commercial clammers. Out of the 1817 clams harvested, 66 were juveniles, 2 pre-littlenecks, 1741 littlenecks, 6 cherrystones and 1 chowder.

The life span of the hard clam, *Mercenaria mercenaria*, is estimated to be 40 years (Hopkins 1930; Comfort 1957). Although clams were aged to a maximum of 40 years in this study, most clams were less than 10 years of age (Fig. 3). The maximum hard clam age found in this study agrees with those found in other clam populations (Table 3).

Chowders are the dominant size class of clam populations of coastal Georgia. This is in agreement with the results of a clam resource survey of Wassaw Sound (Walker, Fleetwood, and Tenore 1980) and of the coastal waters of Georgia (Godwin 1968; Walker and Rawson 1985). The results differ from a clam resource survey in South Carolina where littlenecks were found to dominate (Anderson, Keith, Mills, Bailey, and Steinmeyer 1978). The difference between states may be attributed to the presence or absence of a viable clam fishery. In South Carolina, a viable fishery exists and the larger and older clams have probably been fished out over time. Reduction of larger size and age classes of clams due to fishing pressure was also seen in this study (Fig. 3). On the other hand, chowders dominated in numbers in non-fished areas. With increases in fishing pressure, the percentage of chowders and cherrystones decreased; whereas, the percentages of juvenile clams and littlenecks increased. The low percentage of juvenile (0 and 1 year old) clams in this study may be attributed to sampling error. Clam were collected by hand, an ineffective method of collecting small individuals.

Theoretically, therefore as fishing occurs, older and larger clams will be removed and with time and, according to the level of harvesting pressure,

TABLE 3

Maximum age of the hard clam, *Mercenaria mercenaria*, reported from various geographical areas of the Atlantic and Gulf of Mexico coasts.

Location	Maximum Age in Years	Reference
Fishers Island, NY	15	Malinowski 1985
Barnegat Bay, NJ	8 to 9	Kennish 1978
Delaware Bay, NJ	36	Lutz and Haskin 1985
Virginia	20	Haven and Loesch 1973
Core Sound, NC	32	Peterson *et al.* 1985
Cape Lookout, NC	29	Peterson *et al.* 1983
Coastal Georgia	40	This study
Little Tybee Island, GA	34	Walker 1984a
Kings Bay, GA	25	Quitmyer *et al.* 1985
Boca Ciega, FL*	22	Saloman and Taylor 1969
Christmas Bay, TX**	14	Craig and Bright 1986

* For the Southern hard clam, *Mercenaria campechiensis*

** For the Texas hard clam, *Mercenaria mercenaria texana*

smaller, younger clams will dominate. This has also been observed in the New York area. Within heavily fished areas in Great South Bay, clams were found to be under four years of age (*i.e.*, the age that clams reached marketable size); whereas, areas that are closed to fishing contain older and larger clams with lower proportions of juveniles or littlenecks (Greene 1978). In Barnegat Bay, New Jersey, no clams were found over 9 years of age (Kennish 1980) and Peterson, Duncan, Summerson, and Beal (1985) attributed this absence of older clams to fishing pressure.

In the clam populations of coastal Georgia, mean clam densities ranged from 0 to 151 adult clams per square meter. These densities agree with densities reported in other clam resource surveys in Georgia (Godwin 1967, 1968; Walker *et al.* 1980; Walker and Rawson 1985). Reported clam densities from other areas throughout the United States are given in Table 4. In Georgia, clams occur frequently in dense numbers; however, generally the area of the bed is small and the beds often occur within the creek system in inaccessible areas. For instance, in Wassaw Sound, Georgia, a clam population with a mean of 50 clams per square meter covered an area of approximately 90 m^2.

The clam populations of coastal Georgia consist of both harvested and unharvested populations. In unharvested populations in Georgia, chowders generally dominate in numbers (Godwin 1968, Walker *et al.* 1980, Walker and Rawson 1985) with the population being comprised of older individuals (Walker 1984a, Walker and Stevens 1988), MacKenzie (1979) describes unharvested clam populations as those that exhibit sparse and sporadic setting, declining setting densities of spat, increased predation of juveniles and are comprised mostly of relatively old clams. Malinowski (1985) concludes that even in populations with low rates of annual successful recruitment (due to sporadic setting and/or to predation) into the adult age classes, an unharvested population will ultimately result in dense assemblages of clams with time. From the data presented in this study, Malinowski's characterization of old populations is more applicable to Georgia populations than MacKenzie's. Sporadic and low setting densities are the rule in Georgia (personal observation) regardless of whether or not the population is being harvested. Recruitment is a gradual event in Georgia with spawning possibly occurring over most of the year (Pline 1984). Gonadal studies show that peak spawning in Georgia occurs in fall and spring, but that spawning occurs over a 10-month period (Pline 1984). This may account for the absence of any major sets occurring in Georgia. Thus it appears that a few individuals successfully recruit to the population each year resulting in dense numbers of older clams in unharvested populations over time.

Beal (1983) hypothesized that dense assemblages of neighboring large clams (80 m^{-2}) may protect smaller clams from predation. Kennish (1978) observed clam populations that were without juveniles. He hypothesizes that this indicated an inverse association between adults and juveniles. He further states that adult populations may preclude successful settlement of young clams because of competition for food. Therefore successful recruitment of

TABLE 4

Hard clam, *Mercenaria mercenaria*, densities reported for natural clam populations.

Location	No. m^{-2}	Reference
U.S.A.		
Maquoit Bay, ME	*860	Dow and Wallace, 1951
Barnstable Harbor,MA	1	Sanders *et al.*, 1962
Narragansett Bay, RI	4	Russell, 1972
Greenwich Bay, RI	2 to 12	Stickney and Stringer, 1957
Greenwich Bay, RI	215	Stringer, 1955
Long Island Sound, CT	0.9	MacKenzie, 1977
Northport Bay, NY	6.5	MacKenzie, 1977
Great South Bay, NY	18.4	MacKenzie, 1977
Islip, NY		Buckner, 1979
Open areas	16	
Closed areas	30	
Patchogue Bay, NY	81	Greene, 1978
East Patchogue Bay, NY	16	Greene, 1978
Patchogue Bay, NY	50	Greene, 1978
Barret Beach, NY	16	Greene, 1978
East Islip, NY	11	Greene, 1978
Goose Creek, NY	10	Kaplan *et al.*, 1975
Raritan Bay, NJ	14	MacKenzie, 1977
Raritan Bay, NJ	5 to 11	Campbell, 1965
Little Egg Harbor, NJ	34	Carriker, 1961
Chinocoteague Bay, MD	1	Wells, 1957
Poquoson Flats, VA	5	Loesch and Haven, 1973
Johnson Creek, NC	6.4	Peterson *et al.*, 1983
Back Sound, NC	2 to 10	Peterson *et al.*, 1984
Santee River, SC	18 to 24	Rhodes *et al.*, 1977
North Inlet, SC	6	Dame, 1979
Coastal Georgia	0.1 to 21	Godwin, 1968
Christmas Creek, GA	151	This Study
Wassaw Sound, GA	0 to 100	Walker *et al.*, 1980
Coastal Georgia	0 to 91	Walker and Rawson, 1985
Colorado Lagoon, CA	556	Crane *et al.*, 1975
Christmas Bay, TX	0 to 5.6	Craig and Bright, 1986
Great Britain		
Southampton Waters	6 to 8	Ansell, 1963
Southampton Waters	0.3 to 12.3	Hibbert, 1976

* This population of juveniles was undergoing heavy mortality due to overcrowding.

Mercenaria mercenaria may be regulated by density-dependent factors, *i.e.*, when density of adults is high, juveniles are forced to settle in unoccupied areas (Kennish 1978). Unfortunately, Kennish (1978) gave no density estimates and his population was comprised of individuals less than 9 years old. If one looks at the four densest populations in the Christmas Creek area (Stations 3, 4, 5 and 7, *i.e.*, 74, 151, 86 and 68 clams m^{-2} respectively), only Population 4 would support Kennish's conclusions that dense adult populations preclude successful recruitment. In Population 4, only 1.5% of the clams are less than 12 years old. Thus it would appear that adults may preclude recruitment. Yet in Populations 3, 5 and 7, there are clams in nearly all year classes, suggesting that there has been recruitment every year for the last 10 years into each of these populations. The majority of the populations would support Beal's hypothesis that dense assemblages of large clams protect smaller clams. Populations 3, 5 and 7 are approximately equivalent to his experimental density of 80 m^{-2}. Population 4 has almost twice that density. Thus it appears that the density of adult clams needed to preclude successful recruitment may be much greater than that envisioned by Kennish.

The results of this work are important to the development of the hard clam fishery in coastal Georgia. Firstly, in 38 of 40 clam populations studied, clams grew to marketable size in 2 to 3 years, whereas in the New York area, it requires 4 to 5 years to obtain marketable size. This excellent growth was found throughout the higher saline waters of coastal Georgia. The two populations that exhibited poor growth rate occurred under extreme environmental conditions. Secondly, this excellent growth rate and marketability of this clam makes it an excellent candidate for aquaculture in coastal Georgia. Thirdly, clam populations in Georgia will undergo dramatic changes in size and age-structure as the fishery continues to grow. The larger and older clams will be cropped out of the populations over time. Eventually, clam populations will be dominated by the smaller age classes, *i.e.*, littlenecks.

In terms of the fishermen, populations dominated by littlenecks (most valuable size class in monetary terms) are desirable. In terms of population biology, however, it may not be so desirable. Clam reproductive potential increases with size according to a power function (Peterson 1983). Chowders produce more eggs and sperm than an equivalent number of littlenecks. Since successful recruitment is reflected in only a few clams being added to the population per year, the removal of chowders (probably the major spawners) could eventually harm the fishery. Chowders, when marketable, go for 3 to 4 cents each versus 10 to 30 cents each for littlenecks. Thus while chowders may not be important in monetary terms, their probable reproductive potential may be eliminated through normal fishing practices. The reproductive potential of chowders in Georgia is currently being investigated.

ACKNOWLEDGMENTS

I wish to thank Mr. John Veazey, Drs. Peter Heffernan and Stuart Stevens for their help in collecting clams from the Christmas Creek area and Bruce and Cathy Paulson for their help in

collecting clams at the Crooked River and northern Cumberland Island Stations. I wish to thank Mrs. Jeanette Haley for typing the manuscript. I would especially like to thank Mr. Michael Castagna, Drs. J. Crenshaw, J. Harding, P. Heffernan, and two anonymous reviewers for reviewing the manuscript. The work was supported by the Georgia Sea Grant Program under grant numbers NA80AA-D-00091 and NA84AA-D-00072.

LITERATURE CITED

ANDERSON. W.D., W.J. KEITH, F.H. MILLS, M.E. BAILEY, and J.L. STEINMEYER. 1978. A survey of South Carolina hard clam resources. South Carolina Wildlife and Marine Resources Department, Marine Resources Center, Technical Report. 21, vi + 17p + 15p. Appendix III.

ANSELL, A.D. 1963. *Venus mercenaria* (L.) in Southampton water. *Ecology*. 44:396-397.

BEAL, B.F. 1983. Effects of environment, intraspecific density, predation by snapping shrimp and other consumers on the population in biology of *Mercenaria mercenaria* near Beaufort, North Carolina. Masters Thesis, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina. 177 pp.

BUCKNER, S.C. 1979. Shellfish management in the Town of Islip. Proceedings of a Symposium on Mariculture in New York State. New York Sea Grant Institute and Cornell University. NUSG-I-RP-79-01:13-18.

CAMPBELL, R. 1965. A report on the economically important shellfish resources of Raritan Bay. U.S. Department of Health, Education and Welfare, Public Health Service, Northeast Shellfish Research Center, Narragansett, Rhode Island. 11 pp.

CARRIKER, M.R. 1961. Interrelation of functional morphology, behavior, and autoecology in early stages of the bivalve, *Mercenaria mercenaria. Journal of the Elisha Mitchell Science Society*. 77:168-241.

COMFORT, A. 1957. Duration of life in molluscs. *Proceedings of Malacological Society*. 32:219-241.

CRAIG, M.A. and T.J. BRIGHT. 1986. Abundance, age distributions and growth of the Texas hard clam, *Mercenaria mercenaria texana*, in Texas bays. *Contributions in Marine Science*. 29:59-72.

CRANE, J.M., JR., L.G. ALLEN and C. EISEMANN. 1975. Growth rate, distribution, and population density of the northern quahog, *Mercenaria mercenaria* in Long Beach, California. *California Fish and Game*. 61:82-94.

DAME, R.F. 1979. The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina intertidal oyster reefs. *Proceedings of the National Shellfisheries Association*. 69:6-10.

DOW, R.L. and D.E. WALLACE. 1951. A method of reducing winter mortalities of *Venus mercenaria* in Maine waters. Department of Sea Shore and Fisheries, Augusta, Maine. Research Bulletin 4. 31p.

ELDRIDGE, P.J., W. WALTZ, R.C. GRACY and H.H. HUNT. 1976. Growth and mortality rates of hatchery seed clams, *Mercenaria mercenaria*, in protected trays in waters of South Carolina. *Proceedings of the National Shellfisheries Association*. 66:13-20.

_____, A.G. EVERSOLE and J.M. WHETSTONE. 1979. Comparative survival and growth rates of hard clams, *Mercenaria mercenaria*, planted in trays subtidally and intertidally at varying densities in a South Carolina Estuary. *Proceedings of the National Shellfisheries Association*. 69:30-39.

GODWIN, W.F. 1967. A preliminary survey of a potential hard clam fishery. Georgia Game and Fish Commission. Contribution Series No. 1, Brunswick, Georgia. 23 pp.

_____. 1968. The distribution and density of the hard clam, *Mercenaria mercenaria*, on the Georgia coast. Georgia Game and Fish Commission, Contribution Series No. 10, Brunswick, Georgia. 30 pp.

GREENE, G.T. 1978. Population structure, growth and mortality of hard clams at selected locations in Great South Bay, New York. Master Thesis, State University of New York at Stony Brook, Stony Brook, New York. 199 pp.

HAVEN, D.S. and J.G. LOESCH. 1973. Summary, conclusions and recommendations based on an investigation into commercial aspects of the hard clam fishery and development of commercial gear for the harvest of molluscs. Final Report for PL 88-309, Project 3-124-R, Virginia Institute of Marine Science. Gloucester Point, Virginia 108 pp.

HIBBERT, C.J. 1976. Biomass and production of a bivalve community on an intertidal mudflat. *Journal of Experimental Marine Biology and Ecology.* 25:249-261.

HOPKINS, H.S. 1930. Age differences and the respiration in muscle tissues of mollusks. *Journal of Experimental Zoology.* 52:209-239.

JOHNSON, A.S., H.0. HILLESTAD, S.F. SHANHOLTZER, and G.F. SHANHOLTZER. 1974. An ecological survey of the coastal region of Georgia. National Park Service Scientific Monograph Series. Number 3. 233 pp.

KAPLAN, E.H., J.R. WELKER, M.G. KRAUS and S. McCOURT. 1975. Some factors affecting the colonization of a dredged channel. *Marine Biology.* 32:193-204.

KENNISH, M.J. 1978. Effects of thermal discharges on mortality of *Mercenaria mercenaria* in Barnegat Bay, New Jersey. *Environmental Geology.* 2:223-254.

_____. 1980. Shell microgrowth analysis of *Mercenaria mercenaria* as a type example for research in population dynamics. p. 255-294. In D.C. Rhoads and R.A. Lutz (editors) *Skeletal Growth of Aquatic Organisms.* Plenum Press, WY. 750 pp.

LOESCH, J.F. and D. HAVEN. 1973. Estimated growth functions and size-age relationships of the hard clam, *Mercenaria mercenaria*, in the New York River, Virginia. *The Veliger.* 16:76-81.

LUTZ, R.A. and H.H. HASKIN. 1985. Some observations on the longevity of the hard clam, *Mercenaria mercenaria* (Linne'). *Journal of Shellfish Research.* 5:19 (Abstract).

MacKENZIE, C.L., Jr. 1977. Predation on hard clam (*Mercenaria mercenaria*) populations. *Transactions of the American Fisheries Society.* 106:530-537.

_____. 1979. Management for increasing clam abundance. *Marine Fisheries Review.* 41:10-22.

MALINOWSKI, S.M. 1985. The population ecology of the hard clam, *Mercenaria mercenaria*, in Eastern Long Island Sound. Ph.D. Dissertation, University of Connecticut, Groton, Connecticut. 112 pp.

MENZEL, R.W. 1964. Seasonal growth of northern and southern quahog, *Mercenaria mercenaria* and *M. campechiensis*, and their hybrids in Florida. *Proceedings of the National Shellfisheries Association.* 53:111-119.

NATIONAL MARINE FISHERIES SERVICE. 1977. The molluscan shellfish industries and water quality: problems and opportunities. U.S. Department of Commerce, NOAA, National Marine Fisheries Service, Office of Fisheries Development, Superintendent of Documents., Washington, DC. v + 46 pp.

PETERSON, C.H. 1983. A concept of quantitative reproductive senility: application to the hard clam, *Mercenaria mercenaria* (L.)? *Oecologia.* 58:164-168.

_____, H.C. SUMMERSON and P.B. DUNCAN. 1984. The influence of seagrass cover on population structure and individual growth rate of a suspension feeding bivalve, *Mercenaria mercenaria. Journal of Marine Research.* 42:123-138.

_____, P.B. DUNCAN, H.C. SUMMERSON and B.F. BEAL. 1985. Annual band deposition within shells of the hard clam, *Mercenaria mercenaria*: consistency across habitat near Cape Lookout, North Carolina. *Fishery Bulletin, U.S..* 83:671-677.

_____, _____, _____ and G.W. SAFRIT, Jr. 1983. A mark-recapture test of annual periodicity of internal growth band deposition in shells of hard clams, *Mercenaria mercenaria*, from a population along the southeastern United States. *Fishery Bulletin, U.S..* 81:765-779.

PLINE, M.J. 1984. Reproductive cycle and low salinity stress in adult *Mercenaria mercenaria* L. of Wassaw Sound, Georgia. Masters Thesis, School of Applied Biology, Georgia Institute of Technology, Atlanta, Georgia. 74 pp.

QUITMYER, I.R., H.S. HALE and D.S. JONES. 1985. Paleoseasonality determination based on incremental shell growth in the hard clam, *Mercenaria mercenaria*, and its implications for the analysis of three southeast Georgia coastal shell middens. *Southeastern Archaeology.* 4:27-40.

RHOADS, D.C. and G. PANNELLA. 1970. The use of molluscan shell growth patterns in ecology and paleoecology. *Lethaia.* 3(3):143-161.

_____ and R.A. LUTZ. 1980. *Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change.* New York, Plenum Press. 750 pp.

RHODES, R.J., W.J. KEITH, P.J. ELDRIDGE and V.G. BURRELL, Jr. 1977. An empirical evaluation of the Lesile-Delury method applied to estimating hard clam, *Mercenaria mercenaria* abundance in the Santee River estuary, South Carolina. *Proceedings of the National Shellfisheries Association.* 67:44-52.

RUSSELL, H.J., JR. 1972. Use of a commercial dredge to estimate a hard shell clam population by stratified random sampling. *Journal of the Fisheries Research Board of Canada.* 29:1731-1735.

SALOMAN, C.H. and J.L. TAYLOR. 1969. Age and growth of large southern quahogs from a Florida estuary. *Proceedings of the National Shellfisheries Association.* 59:46-51.

SANDERS, H.L., E.M. GOUDSMIT, E.L. MILLS and G.E. HAMPSON. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnology and Oceanography.* 7:63-79.

STICKNEY, A.P. and L.D. STRINGER. 1957. A study of the invertebrate bottom fauna of Greenwich Bay, Rhode Island. *Ecology.* 38:111-121.

STRINGER, L.D. 1955. Greenwich Bay hard clam productivity studies. U. S. Fish and Wildlife Service, Clam Investigation Conference on Clam Resources. 5:1-9.

WALKER, R.L. 1983. Feasibility of mariculture of the hard clam, *Mercenaria mercenaria* (Linne'), and clam predators in coastal Georgia. *Journal of Shellfish Research.* 3:169-174.

_____. 1984a. Population dynamics of the hard clam, *Mercenaria mercenaria* (Linne'), and its relation to the Georgia hard clam fishery. Masters Thesis, School of Applied Biology, Georgia Institute of Technology, Atlanta, Georgia. 121 pp.

_____. 1984b. Effects of density and sampling time on the growth of the hard clam, *Mercenaria mercenaria*, planted in predator-free cages in coastal Georgia. *The Nautilus.* 98:114.119.

_____ and M.V. RAWSON. 1985. Subtidal hard clam, *Mercenaria mercenaria* (Linne') resources in coastal Georgia. Georgia Marine Science Center, Technical Report. 85-1. 164 pp.

_____ and S.A. STEVENS. 1988. Hard clam, *Mercenaria mercenaria* (Linne'), resources of Christmas Creek, Little Cumberland and Cumberland Island. Georgia Department of Natural Resources. Contribution Series No. 41. 30 pp.

_____, M.A. FLEETWOOD, and K.R. TENORE. 1980. The distribution of the hard clam, *Mercenaria mercenaria* (Linne'), and clam predators in Wassaw Sound, Georgia. Georgia Marine Science Center, Technical Report. 80-8, 59 pp.

WELLS, H.W. 1957. Abundance of the hard clam, *Mercenaria mercenaria*, in relation to environmental factors. *Ecology.* 38:123-128.

Contributions in Marine Science. (1989) Vol. 31:77–94.

MORTALITY AND CONDITION OF THE AMERICAN OYSTER IN GALVESTON BAY, TEXAS

Thomas M. Soniat, Lorene E. Smith and Michael S. Brody[1]

Department of Biological Sciences
University of New Orleans
Lakefront, New Orleans, Louisiana 70148

ABSTRACT

Mortality and condition of the American oyster, *Crassostrea virginica*, were studied on sixteen 0.1-hectare sites on reefs in Galveston Bay, Texas. Oyster mortality was evaluated by three methods—the box-count method (number of articulated empty shells/number of articulated empty shells plus live oysters), the catch-curve method (log frequency versus size), and by tray experiments in which open tray, closed tray, and predator-inclusion trays (in which an oyster drill, *Thais haemostoma* was enclosed in each) were used. Estimates of average annual mortality based on the catch-curve method (0.76) and open-tray analyses (0.61) were similar but these methods contrasted with box counts. Mortality determined by the catch-curve method did not correlate significantly with oyster density; however, mortality was high and density values were low at the extremes of oyster distribution. A weight/volume condition index was positively correlated with a gonadal index. Glycogen concentration was negatively correlated with salinity whereas intensity (*i.e.*, weighted incidence, WI) of infection by *Perkinsus marinus* was positively correlated with salinity. The glycogen values of oysters from reefs with greater than a light infection level (WI > 2.00; $n = 7$) showed a significant negative correlation with WI.

High mortalities were apparently the result of frequent flooding at low salinity sites, but appeared to be caused by the oyster drill and disease (due to the protozoan *P. marinus*) at high-salinity sites. Percentage of boxes is likely related to short-term mortality, whereas mortality estimated by the catch curve method is a measure of longer term mortality. Percentage of boxes was highest at the highest salinity sites where disease was most prevalent. Glycogen concentrations decreased as salinity increased, which may be related to more favorable trophic conditions in fresher water and/or higher levels of disease in saltier water.

INTRODUCTION

Factors of mortality in the American oyster *Crassostrea virginica* (Gmelin), which ultimately determine the distribution of the species, are well documented (Butler 1954a; Galtsoff 1964). Along the Gulf of Mexico, the major

[1]Environmental Protection Agency, Office of Toxic Substances (TS-798), 401 Street SW, Washington,D.C., 20460

causes of mortality in high-salinity areas are the Southern oyster drill *Thais haemostoma* L. and the pathogenic protozoan *Perkinsus (=Dermocystidium) marinus* (Mackin, Owen and Collier 1950). In areas with a mean salinity of 15‰ or more, oyster drills sometimes deplete an oyster reef in a short time (Burkenroad 1931; St. Amant 1938; Schechter 1943; Butler 1953, 1954a, 1954b; Gunter 1955, 1979; Menzel, Hulings, and Hathaway 1957; Galtsoff 1964; Van Sickle, Barrett, Ford, and Gulick 1976). Severe mortalities due to *P. marinus* have been reported in oysters from all the Gulf states (Mackin, Owen, and Collier 1950; Mackin 1953; Ray, Mackin, and Boswell 1953; Ray 1954, 1966a; Dawson 1955; Quick and Mackin 1971; Beckert, Bland, and May 1972; Ogle and Flurry 1980; Soniat 1985). Because of the importance of drill predation and *Perkinsus* disease to oyster populations, Cake (1983) included these factors in a Habitat Suitability Index (HSI) model for the American oyster in the Gulf of Mexico.

In the condition index of Hopkins (1949), which has often been used in the assessment of oyster quality and marketability, dry weight of the oyster meat is compared with the volume of the shell cavity (Engle 1950; Haven 1961; Galtsoff 1964; Walne 1970; Ogle 1979; Lawrence and Scott 1982; Soniat and Ray 1985). Hopkins, Mackin, and Menzel (1954), using the measures of condition index and glycogen content, found that the quality of Louisiana oysters was highest in late winter and early spring and lowest in late summer and early fall. Monitoring of the gonad in the form of a gonadal index is also important in the study of the annual cycle of oyster condition (Soniat and Ray 1985). Some environmental factors that influence oyster condition include population density, availability of food, water temperature and salinity, character of the substrate, and pollutants (Engle 1950; Korringa 1952; Butler 1954a; Haven 1961; Galtsoff 1964; Scott and Lawrence 1982). Parasitism by *P. marinus* sometimes also affects the condition index and glycogen content (Mackin, 1951; Ray *et al.* 1953; Ray and Chandler 1955; Quick and Mackin 1971).

The purposes of this study were to:

(i) determine mortality rates and condition of oyster from reefs in Galveston Bay, Texas,

(ii) evaluate the strength of the relationship between measures of oyster mortality and measures of oyster condition, and

(iii) compare various methods for estimating mortality and condition.

MATERIALS AND METHODS

Study Area and Sample Sites

The Galveston Bay estuarine system is located on the northeastern Texas coast. The bay complex has a mean depth of about 2.2 m (range, 0.5 to 3 m), a water surface area of 135,170 hectares, and a volume of $3 \times 10^9 m^3$ (Copeland and Bechtel 1971). The estuarine system consists of upper and lower Galveston Bay, East Bay, West Bay, and Trinity Bay (Fig. 1). Oysters were collected from 16 reefs of the Galveston Bay complex from 16 May to 11 June 1985, and tray experiments were conducted from 10 June to 11 August 1985.

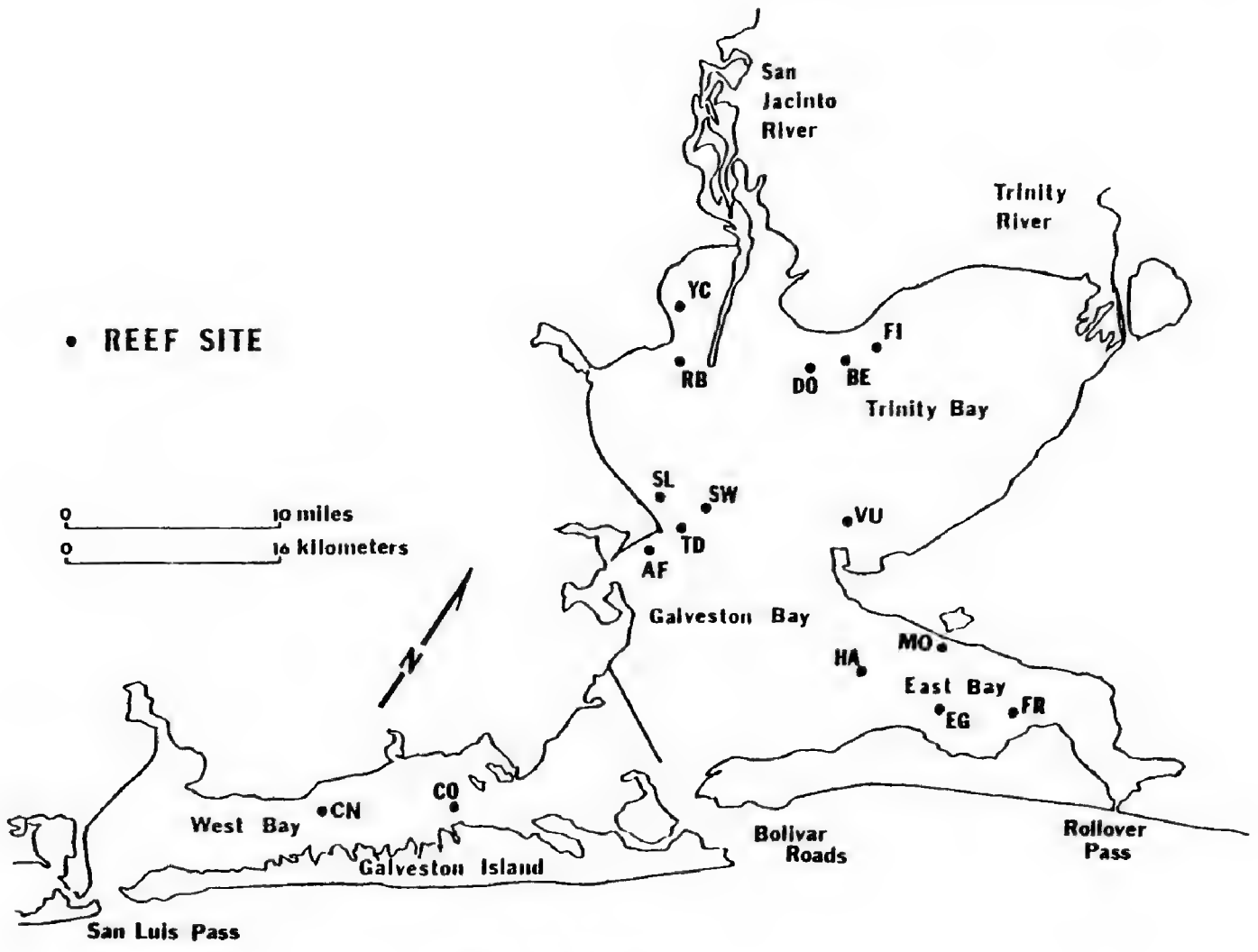


FIG. 1. The Galveston Bay Complex showing sampling sites (reefs). YC = Yacht Club, RB = Red Bluff, DO = Dow, BE = Beasley's, FI = Fisher's, SL = San Leon, SW = Switchover, TD = Todd's Dump, AF = April Fool, NR = North Redfish, SR = South Redfish, VU = Vingt et un, HA = Hannah's, MO = Moody's, EG = Elm Grove, FR = Frenchy's, CA = Carancahua (first sampling), CN = Carancahua (second sampling), CO = Confederate.

Population Studies

Populations were estimated in May and June 1985 on sixteen 0.1-hectare reef sites (Fig. 1). Living oysters and boxes (articulated empty shells) were collected by a diver, who sampled within a 0.25m^2 grid. Live oysters and boxes within 30 such sample grids per study site were removed, counted, and separated into 2.5-cm size classes. An index of precision (D) — a ratio of the standard error to the arithmetic mean — was calculated to determine the error associated with the density estimate (Elliot 1977). The percent boxes (PB)was determined, and catch curves, which are useful in visualizing oyster mortality at the different reefs, were constructed for most of the study sites (Mackin 1961a). The curves were constructed as a graph of logarithm of the percent frequency of occurrence of oysters in 25-cm size classes. Survival rate (S) was calculated as:

$$S = \frac{\Sigma_{a=o}^{w} aN_a}{\Sigma_{a=o}^{w} N_a + \Sigma_{a=o}^{w} aN_a - 1}$$

where N_a = the number of individuals in each size class, $\Sigma_{a=o}^{w} N_a$ is the total number in the sample, and $\Sigma_{a=o}^{w} aN_a = o + N_1 + 2N_2 + \ldots wN_w$ (Robson and Chapman 1961).
Mortality rate (MORT; Table 1) was calculated as $1 - S$.

Tray Experiments

Tray experiments were conducted at a high-salinity site (Confederate Reef = CO), a moderate salinity site (April Fool Reef = AF) and a low salinity site (Beasley's Reef = BE). The trays (area, $0.25m^2$) were constructed of 1.2-cm mesh galvanized hardware cloth; 10 oysters were placed in each tray. Open trays had no lids and were thus easily accessible to predators; closed trays were covered with hardware cloth. Spat trays were open trays in which 25 clean oyster shells, used as a substrate for settling oyster larvae, were placed; predator inclusion trays were closed trays in which one Southern oyster drill *Thais haemostoma* L. was included. Three open trays, three closed trays, and three spat trays were used at all three sites, but predator inclusion trays were used only at the high salinity site (CO). When the trays were checked and cleaned (at about biweekly intervals), dead oysters were counted and replaced. Oysters of commercial size (7.6-12.5 cm) were used in all the tray experiments.

Condition Index

Twelve adult oysters, randomly sampled from each reef site and cleaned of debris and fouling organisms, were used for the determination of condition index, parasitism, gonadal index, and glycogen content. The total intact volume of the oysters (pooled) was determined by water displacement in a spouted container. The oysters were then removed from the container, numbered, and "length" (umbo to bill) of the right valve of individual oysters was measured. The length range was 6.1 to 12.5 cm. The oysters were shucked, the meats were placed on wire mesh grids to drain, and the valves were retained for pooled volume measurement by water displacement. The total internal cavity volume of the 12 oysters could then be calculated by subtracting the total volume of the valves from the total intact oyster (pooled) volume (Galtsoff 1964).

To determine dry weight, we oven-dried three pooled 5-g samples of homogenized tissue in tared watch glasses at 80 - 85°C for 48 hours. After the samples were weighed, they were again dried and weighed to constant weight on a top-loading electronic balance to the nearest 0.01 g. The dry weight of the 12 oysters was calculated and used to determine the Condition Index of Hopkins (1949) as follows:

$$\text{Condition Index} = \frac{\text{total dry weight (g)}}{\text{shell cavity volume (ml)}} \times 100$$

Parasitism

We removed a piece of mantle tissue of about 4 mm^2 from near the ventral edge of the labial palps to determine the intensity infection by the oyster parasite *Perkinsus marinus*. The parasite was detected by using the thioglycollate culture method of Ray (1966b), and an intensity code value of 0 (uninfected) to 6 (heavily infected) was assigned to each tissue sample (Quick and Mackin 1971). Percent infection and the mean disease intensity, expressed as the weighted incidence (WI), were calculated for each reef according to the equation of Mackin (1961b):

$$\text{WI} = \frac{\text{Sum of disease code numbers}}{\text{numbers of oysters}}$$

Gonadal Condition

The diameter of the adductor muscle and gonadal thickness were measured with vernier calipers. Each oyster was cut with a razor blade across the gonad while it was held above a tared 250-ml beaker. The beaker collected internal fluids to be included in the determination of meat

wet weight. To standardize the gonadal thickness of oysters of different sizes, we calculated a gonadal index (Soniat and Ray 1985) as follows:

$$\text{Gonadal Index} = \frac{\text{average gonadal thickness (mm)}}{\text{average diameter of adductor muscle (mm)}} \times 100$$

A gonadal smear was examined microscopically for the presence of eggs or sperm (Loosanoff 1942). Percent "spawnability" was determined as the percent of sexually developed oysters in the sample (Ogle 1979).

Glycogen

The tared beaker containing the meats of the 12 oysters was weighed on a top-loading electronic balance to the nearest 0.01 g. The oyster meats were then homogenized in a blender for 4 minutes at low speed and 1 minute at high speed (Burklew 1971). Three 5-g subsamples of the homogenate were analyzed for glycogen content (expressed as percent of oyster dry weight) by the extraction technique of Burklew (1971), which is a modification of the methods of Calderwood and Armstrong (1941) and Seifter, Dayton, Novic, and Muntwyler (1950). A Beckman DB Spectrophotometer was used to determine glycogen colorimetrically; glucose was used as a standard.

Statistical Analysis

All statistical analyses were conducted with the Statistical Analysis System package (Helwig and Council 1979) installed on a Vax 8600 computer at the University of New Orleans.

RESULTS

Oyster density ranged from 0.27/m^2 at Carancahua Reef to 52/m^2 at Confederate Reef (Table 1). The error of the density measure was generally less than 20% ($D < 0.20$), yet D values ranged from 0.11 at Beasley's and Moody Reefs to 0.68 at Carancahua Reef (Table 1). Percentage of boxes averaged 5.4% and ranged from 0% (Beasley's and Hannah's Reefs) to 33.3% (Carancahua Reef). Annual mortality averaged 0.77 for all reefs, and ranged from 0.99 (Elm Grove Reef) to 0.54 (Todd's Dump Reef).

Oyster condition, as measured by the condition index (CI), was highest at Confederate Reef (11.5) and lowest at Red Bluff Reef (5.8); mean CI for all reefs was 6.9 (Table 1). Condition index was significantly correlated ($\tau = 0.437), p = 0.025), N = 15$; Table 3) with the gonadal index (GI), which ranged from 5.3 (Frenchy's Reef) to 28.0 (Vingt et un Reef) with a mean of 16.5.

Weighted incidence (WI) of disease (range 0-3.40, mean = 1.43; Table 2) was highest at high salinity sites (*e.g.* Confederate and Carancahua Reefs) and lowest at low salinity sites (*e.g.* Dow and Beasley's Reefs). In fact, one of the strongest correlations in the study was between WI and salinity ($\tau = 0.570, p = 0.003, N = 16$; Table 3). Weighted incidence also showed a close significant correlation with percentage of boxes ($\tau = 0.621, p = 0.001, N = 16$; Table 3).

Glycogen averaged 12.4% of oyster dry weight for the sampling period and ranged from 4.8% for oysters sampled from Elm Groove Reef to 21.1% for those at Vingt et un Reef (Table 1). Glycogen content decreased as

TABLE 1

Sample date, oyster density (number/m^2), index of precision (D), percentage of boxes (PB), percent mortality (MORT), condition index (CI), gonadal index (GI), weighted incidence (WI), glycogen concentration (GLY, percent dry weight), temperature (TEMP, °C), and salinity (SAL, ‰) from the various sample sites. Abbreviations for the study sites are defined in the caption for Fig. 1.

SITE	DATE	DENSITY	D	PB	MORT	CI	GI	WI	GLY	TEMP	SAL
AF	5/25/85	25.87	0.27	8.9	0.58	6.3	16.6	3.0	14.1	27.0	13.0
BE	6/ 9/85	34.93	0.11	0.0	0.74	6.8	17.5	0.00	15.0	29.5	7.5
CO	5/16/85	52.00	0.19	10.5	0.74	11.5	27.7	3.40	5.6	27.0	24.0
CN	6/11/85	0.27	0.68	33.3	---	7.5	16.0	3.33	6.3	29.0	31.0
DO	5/28/85	25.20	0.13	0.5	0.72	6.6	15.8	0.00	17.7	27.0	5.5
EG	6/ 3/85	18.67	0.15	0.7	0.99	6.3	17.7	0.08	4.8	29.0	12.0
FI	5/19/85	2.27	0.29	5.9	0.93	---	24.5	0.08	---	26.0	3.5
FR	6/ 4/85	11.07	0.22	1.2	0.86	6.0	5.3	0.17	11.8	29.0	12.0
HA	5/20/85	3.87	0.25	0.0	0.80	7.3	14.6	0.83	6.6	25.0	12.5
MO	6/ 8/85	18.27	0.11	1.4	0.90	7.1	13.2	0.00	13.2	29.0	11.0
RB	6/ 6/85	44.40	0.18	4.0	0.64	5.8	15.4	1.75	11.3	29.5	8.5
SL	5/27/85	13.37	0.16	4.8	0.84	6.0	11.9	2.08	16.0	29.0	13.5
SW	5/22/85	17.47	0.14	9.7	0.77	6.2	9.4	3.17	9.7	25.0	12.5
TD	5/18/85	4.67	0.20	2.8	0.54	6.2	11.2	2.8	18.8	24.5	12.0
VU	5/23/85	23.33	0.19	0.5	0.70	7.5	28.0	0.08	21.1	26.0	3.5
YC	6/ 6/85	45.47	0.19	2.9	0.78	6.5	19.1	2.17	13.4	30.0	7.5

salinities increased (τ = -0.429, p = 0.028, N = 15; Table 3). Glycogen concentrations were not significantly related to any of the biotic factors or to water temperature (Table 3).

Results of the tray experiments are presented in Table 2. Data from the spat trays are not given since no spatfall occurred. Mortality was lower in closed than in open trays and was highest in the predator inclusion trays. Mortality was higher at the moderate salinity site (April Fool Reef, 13‰) than at the high-salinity site (Confederate Reef, 24‰).

Four extreme patterns (and intermediate ones) were observable from the size-class analysis of living oysters (Fig. 2). Some reefs (Red Bluff, Yacht Club) had many size classes ($\geq$ 4) and many oysters ($>$ 100), whereas other reefs had few size classes and few oysters (Carancahua Reef). Many size classes and few oysters were found at Fisher's Reef and few size classes and many oysters were present at Elm Groove Reef.

Catch curves for the various reefs are shown in Fig. 3. They typically have an ascending left limb and a descending right limb. The steepness of the descending right limb of catch curve is in estimate of mortality. Thus, greatest mortalities are observable at Elm Grove; Fisher's and Moody's Reefs, whereas lowest mortalities are found at Todd's Dump and April Fool Reefs.

Correspondence was good between mortality as measured by the catch-curve method and that estimated from the tray experiments. Average annual mortality was about 0.61 (average weekly mortality $\times$ 52 weeks/yr) from

TABLE 2

Percentage of oysters dead in trays from a high salinity site (Confederate Reef = CO), a moderate salinity site (April Fool Reef = AF) and a low salinity site (Beasley's Reef = BE). Open trays were those without lids which allowed for ready access by predators. Closed trays were designed to exclude predators, and predator inclusion trays were those in which an oyster drill was placed in a closed tray. Ten oysters were placed in each of three trays (T1 = tray 1, T2 = tray 2, T3 = tray 3). Occasional missing oysters were not considered in the calculation of "percent dead". Trays were checked at approximately biweekly intervals. Dates listed are times when the trays were checked. Predator inclusion experiments were conducted only at Confederate Reef. Dashes are used to indicate no data. Summary statistics (means) are included at the bottom of the table.

SITE	DATE	OPEN TRAYS			CLOSED TRAYS			PREDATOR INCLUSION TRAYS		
		T1	T2	T3	T1	T2	T3	T1	T2	T3
CO	6/25/85	10	10	0	10	10	0	10	20	14
AF	6/25/85	14	10	0	13	0	0	--	--	--
BE	6/25/85	0	0	0	13	0	0	--	--	--
CO	7/9/85	10	0	0	0	0	0	10	0	0
AF	7/11/85	10	10	0	10	0	0	--	--	--
BE	7/11/85	0	0	0	0	0	0	--	--	--
BE	7/25/85	0	0	0	0	0	0	--	--	--
AF	7/25/85	--	0	0	0	0	0	--	--	--
CO	7/26/85	0	0	10	0	0	0	0	10	0
CO	8/ 6/85	0	0	0	0	0	0	10	0	0
AF	8/ 8/85	0	0	--	10	0	10	--	--	--
BE	8/ 8/85	0	0	0	0	0	0	--	--	--
CO	8/21/85	0	0	0	0	20	0	20	0	20
AF	8/22/85	10	0	11	0	10	0	--	--	--
BE	8/22/85	0	0	0	0	0	0	--	--	--
Summary statistics (means)										
CO			2.7			2.0			7.6	
AF			4.3			3.5			--	
BE			0.0			0.9			--	

open trays (Table 2) versus 0.77 from the catch curve method (MORT). In contrast, the average percentage of boxes was only 5.4%. No significant relationship between catch-curve mortality (MORT) and oyster density was found ($\tau = -0.249, p = 0.198, N = 15$).

DISCUSSION

An analysis of size class distributions (Fig. 2), mortality rates (Table 1), and tray data (Table 2) is useful in inferring specific causes of mortality. Oysters from Trinity Bay were generally smaller and populations there were composed of fewer size classes than were those from other parts of the bay complex. As judged from the tray data from Beasley's Reef (Table 2), little mortality occurred on reefs in Trinity Bay during the study period. Substantial mortalities were recorded (Table 2) at higher salinities (Confederate and April Fool Reefs) where drills and disease were prevalent (T.M. Soniat and

TABLE 3

Kendall Tau Beta correlation coefficients, significance levels, and number of samples. Abbreviations for the variable names are given in Table 1.

	MORT	DEN	CI	GI	WI	GLY	SAL	TEMP
PB	-0.077	-0.084	-0.127	0.017	0.621	-0.240	0.340	-0.018
	0.691	0.562	0.517	0.928	0.001	0.215	0.037	0.926
	15	16	15	16	16	15	16	16
MORT		-0.249	0.011	-0.038	-0.315	-0.375	-0.020	0.163
		0.198	0.956	0.843	0.110	0.062	0.920	0.419
		15	14	15	15	14	15	15
DEN			0.068	0.317	-0.017	0.029	-0.154	0.340
			0.728	0.087	0.928	0.882	0.414	0.080
			15	16	16	15	16	16
CI				0.437	0.010	-0.126	0.000	-0.136
				0.025	0.960	0.518	1.000	0.506
				15	15	15	15	15
GI					-0.051	-0.067	-0.274	0.090
					0.786	0.729	0.147	0.645
					16	15	16	16
WI						-0.262	0.570	-0.138
						0.179	0.003	0.486
						15	16	16
GLY							-0.429	-0.123
							0.028	0.541
							15	15
SAL								-0.064
								0.745
								16

M.S. Brody unpublished observation). In contrast, high mortalities at low salinity sites were the result of frequent freshwater flooding (T.M. Soniat and M.S. Brody, unpublished observation) which, as compared with the relatively unrelenting pattern of mortality at high salinity sites, is highly intermittent.

As expected, mortality from tray experiments (Table 2) was lower in closed than in open trays; it was highest in the predator inclusion trays. Unexpect-

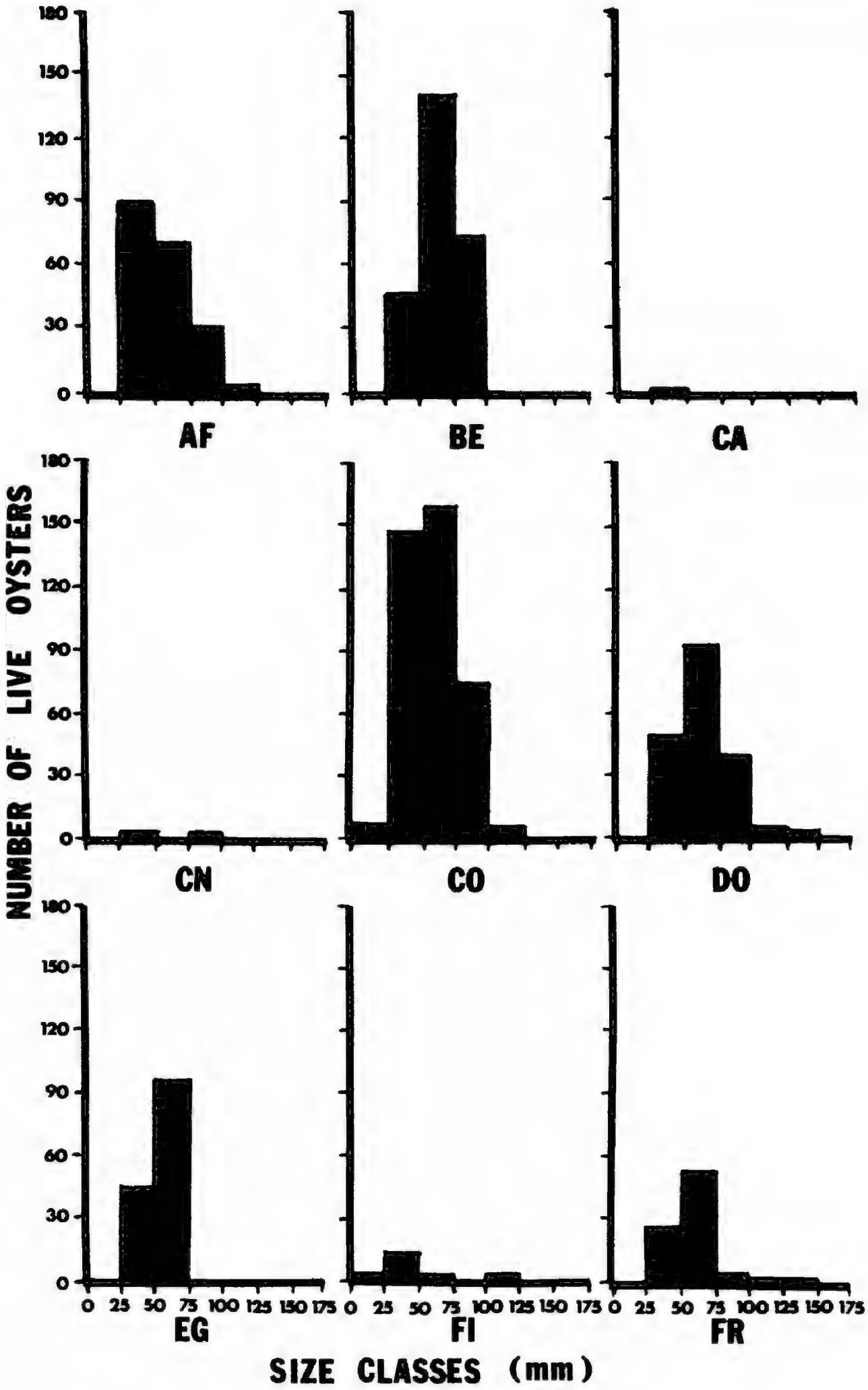


FIG. 2. (PART 1) The number of live oysters in 25-mm size classes from the different reefs. Abbreviations for the reefs are defined in the caption for Fig. 1.

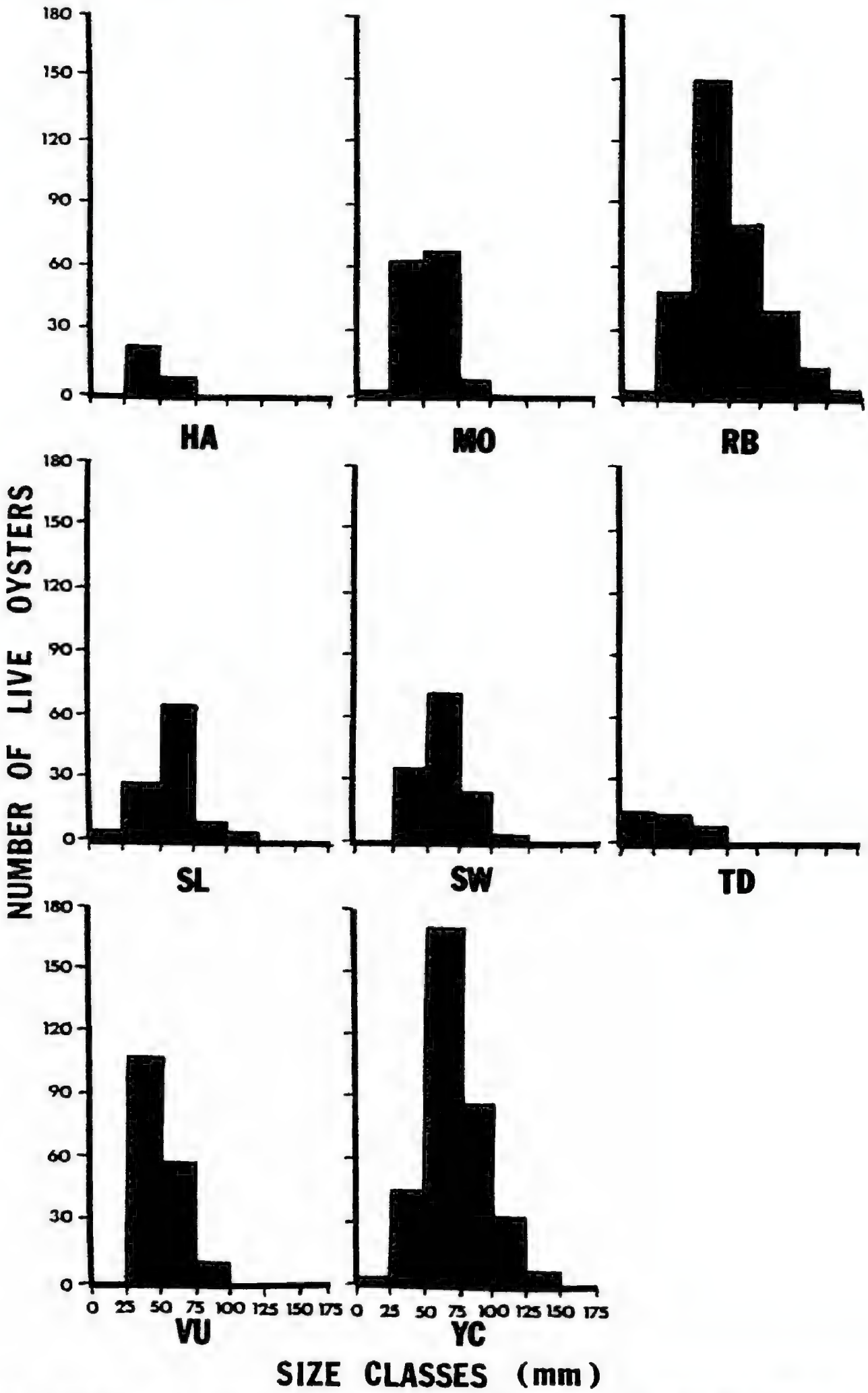


FIG. 2. (PART 2) The number of live oysters in 25-mm size classes from the different reefs. Abbreviations for the reefs are defined in the caption for Fig. 1.

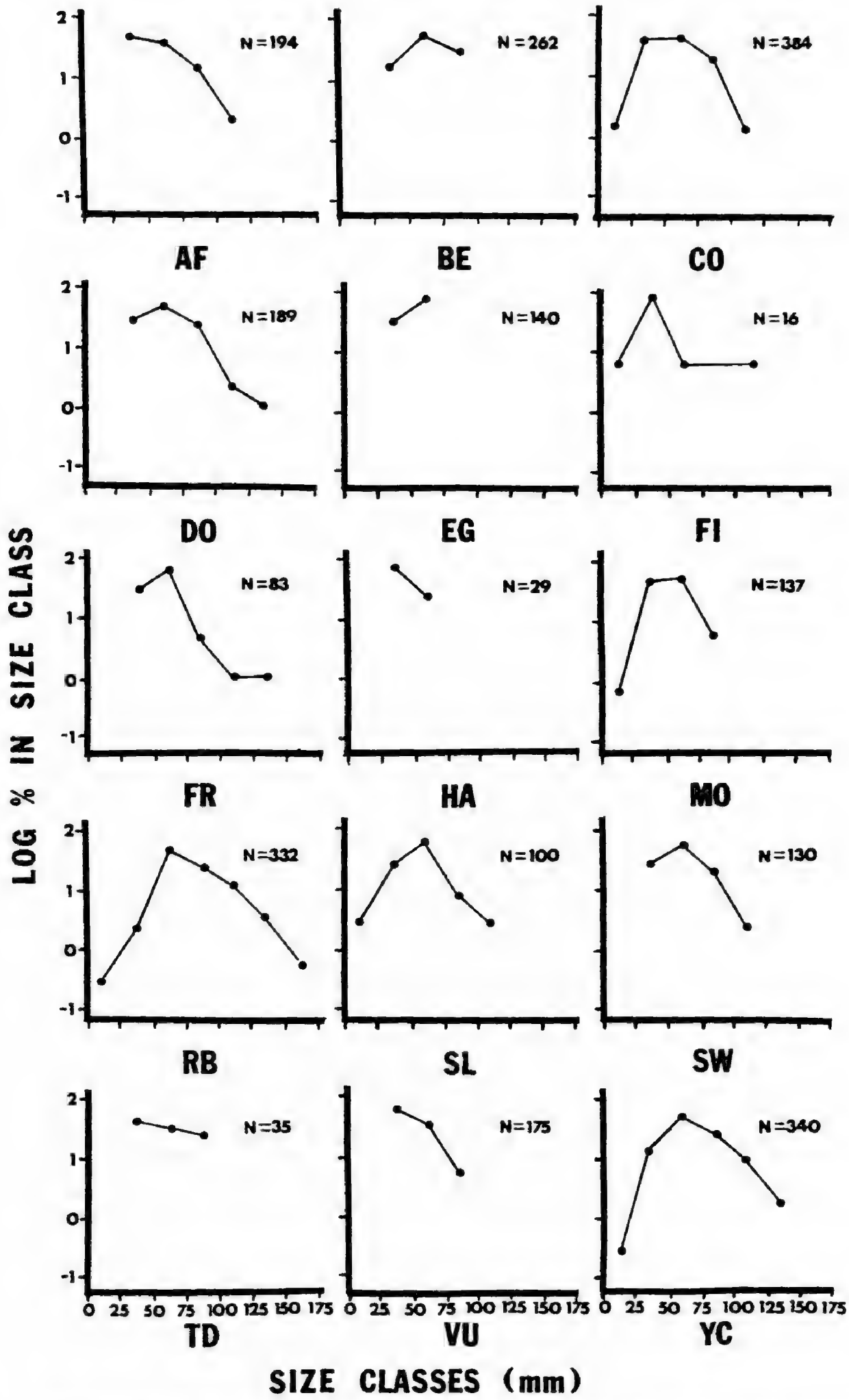


FIG. 3. Catch curves for the various reefs. The catch curves show the frequency of occurrence (y-axis) of oysters in 25-mm size classes (x-axis). N = the number of oysters upon which the curve is based. Abbreviations for the reefs are defined in the caption for Fig. 1.

edly, mortality was higher at the moderate salinity site (April Fool Reef; 13‰) than at the high salinity site (Confederate Reef; 24‰). However, *Perkinsus* disease and drills were present at both April Fool and Confederate Reefs (T.M. Soniat and M.S. Brody, unpublished observation) where the mortality was relatively high, and absent at Beasley's Reef, where the mortality was low.

Percentage of boxes, as stated by Mackin (1961a), is sometimes used as a quick estimate of mortality in the absence of planting and harvesting data, or the long-term use of trays. As Mackin (1961a) pointed out, the "box count" method is not a measure of mortality rate *per se*, since there is no indication of the time required to produce the boxes observed or of the time taken for the boxes to cease being boxes. One might expect a positive relationship to exist between percentage of boxes and mortality rate as calculated from the catch-curve method (CCM), but none was shown. A Kendall-Tau correlation (τ) between percentage of boxes and mortality was not significant ($\tau = -0.077$, $p = 0.691$, $N = 15$; Table 3). Thus, percentage of boxes was neither a mortality measure nor (at least in the present study) correlated with mortality as measured by the catch-curve method (Robson and Chapman 1961; Mackin 1961a). The number of boxes present on a reef is probably related to recent mortality (S.M. Ray, personal communication), whereas mortality estimated by the catch-curve method is a measure of the longer term mortality.

Seasonal changes in glycogen content, gonadal index, condition index, and the level of parasite infection were determined in several previous studies of American oysters (*e.g.*, Hopkins *et al.* 1954; Engle 1958; Haven 1961; Soniat 1982; Soniat and Ray 1985).

Three of the highest glycogen values were from Trinity Bay: Vingt et un Reef, 21.1%; Dow Reef, 17.7%; and Beasley's Reef, 15.0%. This region of the Galveston Bay estuarine complex has been subjected to frequent freshwater flooding (Hofstetter 1977, 1983). Oysters have been found to "fatten" rapidly after floods; the inorganic nutrient load of the freshwater influx may be an important factor in stimulating phytoplankton production (Nelson 1947; Korringa 1952; Gunter 1953). Decreases in freshwater input have been cited as perhaps contributing to reduced oyster condition (Hofstetter 1982). Although prolonged periods of freshwater result in high oyster mortality, American oysters can survive for a limited time in salinities of less than 5‰. According to Hofstetter (1977), oysters of the Galveston Bay estuarine complex have survived in salinities of 2‰ or less for at least 4 weeks when water temperatures were 20°-27°C. Thus survivors of flooding or new recruits to the reefs of Trinity Bay could have benefited from the freshwater input of the Trinity River and smaller watersheds.

Glycogen reserves, high at the initiation of gametogenesis, often decline as gametes develop in marine bivalves (Galtsoff 1964; Gabbott 1975; Bayne 1976; Sastry 1979); under favorable conditions, however, both glycogen and lipids accumulate in the oyster, and growth and gametogenesis can occur simultaneously when food is abundant (Walne 1970; Gabbott 1976). Oysters at Todd's Dump, a reef in lower Galveston Bay (Fig. 1), had a high glycogen content (18.8%) and a low spawnability (58%; see Smith1986). The oysters of

Todd's Dump were perhaps at the point in their annual cycle where the gonads were still maturing, and glycogen content was still high. Spawnability was also 58% at Frenchy's Reef (see Smith 1986), but oysters there lacked high glycogen content noted in those at Todd's Dump. The low gonadal index (GI) in oysters from Frenchy's Reef (5.3, the lowest GI at the reefs sampled) indicated that the oysters there had recently spawned, and the glycogen reserves had not yet been restored. Although glycogen reserves may be used during gametogenesis (Galtsoff 1964; Gabbott 1975; Bayne 1976; Sastry 1979), glycogen values there showed no significant correlation with the gonadal index.

Glycogen content did not correlate significantly with condition index. Correlation between condition index and glycogen content was also poor in a study of the two oyster condition measures made by Ingle (1949). Soniat and Ray (1985) reported a positive correlation between oyster condition index and carbohydrate levels and also between condition index and lipid levels on one reef over a 1-year period. A possible reason for the low correlation in this study was that, just before spawning, a greater proportion of the oyster's body weight would be composed of germinal tissue low in glycogen (Gabbott 1975; Newell and Bayne 1980). Condition index could therefore remain high until spawning, whereas glycogen content would already be declining due to the proliferation of the gametes at the expense of glycogen reserves. Condition index values at Confederate Reef and Carancahua Reef were among the highest observed (11.5 and 7.5), but the glycogen values there were among the lowest.

Two of the lowest glycogen values in this study were found in the oysters from reefs of West Bay: 5.6% at Confederate Reef and 6.3% at Carancahua. A contributor to these low glycogen levels may have been the high incidence of infection with *Perkinsus marinus*. Mackin (1961a) reported that the depletion of glycogen in heavily infected oysters is a result of the parasite's destruction of Leidig cell tissue and the replacement of this tissue with fibrous tissue and leukocytes. Glycogen values for oysters from all the reefs in our study showed a negative trend with increasing weighted incidence (WI), but this trend was not significant at the $p < 0.05$ level. However, the glycogen values of oysters from reefs with greater than a light infection level (WI > 2.00; $n = 7$) showed a significant negative correlation with WI ($\tau = -0.714$, $p = < 0.05$) According to Mackin (1961a), light infections have little effect on the host oyster.

Sexually mature oysters were present at each of the reefs sampled. Water temperatures, ranging from 24.5° to 30°C, were suitable for spawning (Ingle 1951; Hayes and Menzel 1981; Cake 1983). Changes in the gonad during the oyster's annual cycle were described by Loosanoff (1942). When the gonad is ripe it is the adult oyster's largest organ, but the thickness of the gonadal layer decreases during the spawning period as gametes are discharged. In a spent oyster the gonadal index, glycogen content, and condition index are all low (Hopkins *et al.* 1954; Galtsoff 1964; Soniat and Ray 1985). The gonadal index (GI) was lowest (5.3) at Frenchy's Reef (Table 1), and highest (28.0) at Vingt et un Reef. The salinity of 3.5‰ at Vingt et un Reef was, however, not optimal for

spawning (Cake 1983), although mature gametes were present. In oysters at Dow Reef, exposed to a salinity of 5.5‰, gametes were also mature and spawnability was 100%. Butler (1949) reported that oyster gametogenesis was inhibited at salinities below 6‰; thus, mature gametes may have been retained in oysters of Vingt et un and Dow Reefs because of the low salinity there. Glycogen could then have accumulated in the absence of the demands of renewed gametogenesis.

Condition index was positively correlated with gonadal index. This relationship was not expected at this point in the oyster's annual cycle. Lee, Kurtzman, and Pepper (1960) observed that the dry solids content of the meat of southern oysters was high from March to June, just before the spawning season, and then declined to the yearly low in August. Ruddy, Feng and Campbell (1975) reported that gonadal development was the major factor determining a rise in the oyster weight. The water content of many marine bivalves has been found to be the lowest when the gonads are fully developed; it then increases during spawning (Sastry 1979). Dry weight decreases as the gametes are discharged. Once spawning began in Galveston Bay, gonadal index decreased and condition index and carbohydrate levels continued to decline until the occurrence of a late summer spawning peak (Soniat and Ray 1985). Condition index was not correlated with the weighted incidence of the parasite *Perkinsus marinus*, although other studies have shown that moderate and heavy infections caused loss of meat weight (Ray *et al.* 1953; Ray and Chandler 1955). As in the study of Soniat (1982), the parasite's effects on the oyster condition index may have been obscured by the reproductive cycle, the generally light level of infection, and the pooling of oysters for condition index determination.

The mean weighted incidence (WI) of infection by *Perkinsus marinus* was 1.43 for the study period. The WIs were lower for the reefs of Trinity Bay and East Bay than for upper and lower Galveston Bay and West Bay. The weighted incidence was lowest (0; no infection) for Dow, Moody's and Beasley's Reefs and highest (3.40) at Confederate Reef. The WI of infection by *P. marinus* was strongly correlated with salinity ($\tau = 0.570, p = 0.003$). *Perkinsus marinus* has been shown to be prevalent in waters of high salinity and temperature in many studies (*e.g.*, Mackin *et al.* 1950; Mackin 1951; Ray and Chandler 1955; Soniat 1985). In the present study WI and temperature were not significantly correlated; however, temperature varied little throughout the estuarine system during the short study period. High-salinity waters from the Gulf of Mexico enter the estuary primarily through the Bolivar Roads Tidal Pass. Gulf waters also enter West Bay through the San Luis Pass. Infection was heaviest in West Bay and decreased progressively to lower Galveston Bay to upper Galveston Bay. The discharge of fresh water by the San Jacinto and Trinity rivers is a key factor in the maintenance of low levels of infection in the upper portion of the estuarine complex and East Bay (Hofstetter 1977). Although the salinity range in East Bay may be suitable for *P. marinus*, levels of infection have remained low — perhaps because oyster densities are low there (Hofstetter 1977) and a nearby source of infective agents is lacking. The

density of oysters and their degree of isolation have been reported to influence infection levels (Ray and Chandler 1955; Mackin 1961b).

High mortalities were apparently the result of frequent flooding at low-salinity sites but appeared to be caused by the oyster drill and disease by *Perkinsus marinus* at high salinity sites. Percentage of boxes is likely related to short-term mortality, whereas mortality estimated by the catch curve method is a measure of longer term mortality. Percentage of boxes was highest at the higher salinity sites where disease was most prevalent. The condition index of oysters corresponded directly to the reproductive state (as measured by the gonadal index). Glycogen concentrations decreased as salinity increased, which may be related to more favorable trophic conditions in fresh water and/or higher levels of disease in saltier water.

ACKNOWLEDGMENTS

This study was made possible by the cooperation of many persons and their institutions — in particular Carroll Cordes (U.S. Fish and Wildlife Service); Mike Poirrier and Sam Rogers (University of New Orleans); Winston Menzel (Florida State University); Ed Cake (Gulf Coast Research Laboratory); Bob Hofstetter (Texas Parks and Wildlife Department); and Sammy Ray (Texas A&M University of Galveston). Members of the field research team included Julie Gauthier, Rick Howell, Andy Tirpak, and Susan Vreeland. Funding for this work came primarily from the U.S. Fish and Wildlife Service; other support came from the Louisiana Fisheries Initiative Program.

LITERATURE CITED

BAYNE, B.L. 1976. Aspects of reproduction in bivalve molluscs, pp. 432-448. In M. Wiley, (ed) *Estuarine Processes*, Vol. I. Uses, Stresses, and Adaptation to the Estuary. Academic Press, New York.

BECKERT, H., D.G. BLAND and E.B. MAY. 1972. The incidence of *Labyrinthomyxa marina* in Alabama. *Alabama Marine Resources Bulletin.* 8:18-24.

BURKENROAD, M.D. 1931. Notes on the Louisiana conch, *Thais haemostoma* Linn., in its relation to the oyster, *Ostrea virginica. Ecology.* 12:656-664.

BURKLEW, M.A. 1971. Extraction of glycogen from oysters. Florida Department of Natural Resources Research Laboratory Leaflet Series. Vol. 6, Part 3, No. 4. 2 pp.

BUTLER, P.A. 1949. Gametogenesis in the oyster under conditions of depressed salinity. *Biological Bulletin.* 96:263-269.

———— 1953. The southern oyster drill. *Proceedings of the National Shellfisheries Association.* 44:67-75.

———— 1954a. Summary of our knowledge of the oyster in the Gulf of Mexico. *Fishery Bulletin, U.S.*. 55(89):479-489.

———— 1954b. The southern oyster drill. *Proceedings of the National Shellfisheries Association.* 44:67-75.

CAKE, E.W., Jr. 1983. Habitat suitability index models: Gulf of Mexico American oyster. United States Fish and Wildlife Service. FWS/OBS-82/10.57. 37 pp.

CALDERWOOD, H.N. and A.R. ARMSTRONG. 1941. Determination of glycogen in oysters. *Journal of the Association of Official Agricultural Chemists.* 24:154-165.

COPELAND, B.J. and T.J. BECHTEL. 1971. Species diversity and water quality Galveston Bay, Texas. *Water, Air, and Soil Pollution.* 1:89-105.

DAWSON, C.E. 1955. Observations on the incidence of *Dermocystidium marinum* infection in oysters of Apalachicola Bay, Florida. *Texas Journal of Science.* 7:47-56.

ELLIOT, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwater Biological Association Scientific Publication.* 25:1-160.

ENGLE, J.B. 1950. The condition of oysters as measured by the carbohydrate cycle, the condition factor and the precent dry weight. *Proceedings of the National Shellfisheries Association.* (Convention address) 41:20-25

_____. 1958. The seasonal significance of total solids of oysters in commercial exploitation. *Proceedings of the National Shellfisheries Association.* 48:72-78.

GABBOTT, P.A. 1975. Storage cycles in marine bivalve molluscs: a hypothesis concerning the relationship between glycogen metabolism and gametogenesis. pp. 191-211. In H. Barnes (eds) *Proceedings of the Ninth European Marine Biology Symposium.* Aberdeen University Press, Aberdeen, Scotland.

_____. 1976. Energy metabolism, pp. 121-206. In B.L. Bayne (ed) *Marine Mussels: Their Ecology and Physiology.* Cambridge, England.

GALTSOFF, P.S. 1964. The American oyster *Crassostrea virginica* Gmelin. *Fishery Bulletin, U.S.* 64:1-480.

GUNTER, G. 1953. The relationship of the Bonnet Carre Spillway to oyster beds in Mississippi Sound and the "Louisiana Marsh" with a report on the 1980 opening. *Publications of the Institute of Marine Science.* 3:17-76.

_____. 1955. Mortality of oysters and abundance of certain associates as related to salinity. *Ecology.* 36:601-605.

_____. 1979. Studies of the southern oyster borer, *Thais haemastoma. Gulf Research Reports.* 6:249-260.

HAVEN, D. 1961. Seasonal cycle of condition index of oyster in the York and Rappahannock Rivers. *Proceedings of the National Shellfisheries Association.* 51:42-66.

HAYES, P.F. and R.W. MENZEL. 1981. The reproductive cycle of early setting *Crassostrea virginia* (Gmelin) in the northern Gulf of Mexico, and its implications for population recruitment. *Biological Bulletin.* 139:248-264.

HELWIG, J.T. and K.A. COUNCIL. 1979. *SAS User's Guide.* SAS Institute Inc., Cary, North Carolina. 494 pp.

HOFSTETTER, R.P. 1977. Trends in population levels of the American oyster *Crassostrea virginica* Gmelin on public reefs in Galveston Bay, Texas. Texas Parks and Wildlife Department Technical Reports. 24:1-90.

_____. 1982. Status of the Texas oyster industry. pp. 96-100. In K.K. Chew (ed) *Proceedings of the North American Oyster Workshop, 1981.* Special Publication No. 1. Louisiana State University Division of Continuing Education. Baton Rouge, Louisiana.

_____. 1983. Oyster population trends in Galveston Bay 1973-1978. *Texas Parks and Wildlife Department, Management Data Series.* 51:1-33.

HOPKINS, A.E. 1949. Determination of condition in oysters. *Science.* 110:567-568.

HOPKINS, S.H., J.G. MACKIN and R.W. MENZEL. 1954. The annual cycle of reproduction, growth, and fattening in Louisiana oysters. *Proceedings of the National Shellfisheries Association.* (Convention address) 44:39-50.

INGLE, R.M. 1949. A comparative study of oyster condition. *Science.* 109:593.

_____. 1951. Spawning and setting of oysters in relation to seasonal environmental changes. *Bulletin of Marine Science of the Gulf and Caribbean.* 1:111-135.

KORRINGA, P. 1952. Recent advances in oyster biology. *Quarterly Review of Biology.* 27:266-308.

LAWRENCE, D.R. and G.I. SCOTT. 1982. The determination and use of condition index of oysters. *Estuaries.* 5:23-27.

LEE, C.F., C.H. KURTZMAN, and L. PEPPER. 1960. Proximate composition of southern oysters—factors affecting variability. *Commercial Fisheries Review, U.S.* 22:1-8.

LOOSANOFF, V.L. 1942. Seasonal gonadal changes in the adult oysters, *Ostrea virginica*, of Long Island Sound. *Biological Bulletin.* 82:195-206.

MACKIN, J.G. 1951. Histopathology of infection of *Crassostrea virginia* (Gmelin) by *Dermocystidium marinum* Mackin, Owen, and Collier. *Bulletin of Marine Science of the Gulf and Caribbean.* 1:72-87.

_____. 1953. Incidence of infection of oysters by *Dermocystidium* in the Barataria Bay area of Louisiana. *Proceedings of the National Shellfisheries Association.* (Convention address) 1951:22-35.

_____. 1961a. A method of estimation of mortality rates in oysters. *Proceedings of the National Shellfisheries Association.* 50:41-51.

_____. 1961b. Oyster disease caused by *Dermocystidium marinum* and other microorganisms in Louisiana. *Publications of the Institute of Marine Science.* 7:132-299.

_____, H.M. OWEN and A. COLLIER. 1950. Preliminary note on the occurrence of a new protistan parasite, *Dermocystidium marinum* n.sp. in *Crassostrea virginica* (Gmelin). *Science.* 111:328-329.

MENZEL, R.W., N.C. HULINGS and R.R. HATHAWAY. 1957. Causes of depletion of oysters in St. Vincent Bar, Apalachicola Bay, Florida. *Proceedings of the National Shellfisheries Association.* 48:66-71.

NELSON, T.C. 1947. Some contributions from the land in determining conditions of life in the sea. *Ecological Monographs.* 17:337-346.

NEWELL, R.I. and B.L. BAYNE. 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle *Cardium (= Cerastoderma) edule* (Bivalvia: Cardiidae). *Marine Biology.* 56:11-19.

OGLE, J. 1979. A study of four oyster reefs in Mississippi. *Gulf Research Reports.* 6:261-265.

_____ and K. FLURRY. 1980. Occurrence and seasonality of *Perkinsus marinus* (Protozoa: Apicomplexa) in Mississippi oysters. *Gulf Research Reports.* 6:423-436.

QUICK, J.A., Jr. and J.G. MACKIN. 1971. Oyster parasitism by *Labyrinthomyxa marina* in Florida. Florida Department of Natural Resources Marine Research Laboratory. *Professional Paper Series.* 13:1-55.

RAY, S.M. 1954. Biological studies of *Dermocystidium marinum*, a fungus parasite of oysters. *Rice Institute Pamphlet Special Issue.* 114 pp.

_____. 1966a. Notes on the occurrence of *Dermocystidium marinum* on the Gulf of Mexico coast during 1961 and 1962. *Proceedings of the National Shellfisheries Association.* 54:45-54.

_____. 1966b. A review of the culture method for detecting *Dermocystidium marinum* with suggested modifications and precautions. *Proceedings of the National Shellfisheries Association.* 54:55-69.

_____ and A.C. CHANDLER. 1955. *Dermocystidium marinum*, a parasite of oysters. *Experimental Parasitology.* 4:172-200.

_____, J.C. MACKIN, and J.L. BOSWELL. 1953. Quantitative measurement of the effect of oyster disease caused by *Dermocystidium marinum. Bulletin of Marine Science of the Gulf and Caribbean.* 3:6-33.

ROBSON, D.S. and D.G. CHAPMAN. 1961. Catch curves and mortality rates. *Transactions of the American Fisheries Society.* 90:181-189.

RUDDY, G.M., S.Y. FENG, and G.S. CAMPBELL. 1975. The effect of prolonged exposure to elevated temperatures on the biochemical constituents, gonadal development and shell deposition of the American oyster, *Crassostrea virginia. Comparative Biochemistry and Physiology.* 51B:157-164.

SASTRY, A.N. 1979. Pelecypoda (excluding Ostreidae). pp. 113-292. In A.C. Giese and J.S. Pearse (eds) *Reproduction of Marine Invertebrates*, Vol. 5. Molluscs: Pelecypods and Lesser Classes. Academic Press, New York.

SCHECHTER, V. 1943. Tolerance of the snail, *Thais floridana*, to waters of low salinity and the effect of size. *Ecology.* 24:493-499.

SCOTT, G.I. and D.R. LAWRENCE. 1982. The American oyster as a coastal zone pollution monitor: a pilot study. *Estuaries.* 5:40-46.

SEIFTER, S.S., S. DAYTON, B. NOVIC and E. MUNTWYLER. 1950. The estimation of glycogen with the anthrone reagent. *Archives of Biochemistry.* 25:191-200.

SMITH, L.E. 1986. Habitat suitability and condition of oysters from Galveston Bay, Texas. Masters Thesis. University of New Orleans, New Orleans, Louisiana. 69 pp.

SONIAT, T.M. 1982. Studies on the nutritional ecology and ecological energetics of oysters from Galveston Bay. Ph.D. Thesis. Texas A&M University, College Station, Texas. 162 pp.

_____. 1985. Changes in levels of infection of oysters by *Perkinsus marinus,* with special reference to the interaction of temperature and salinity upon parasitism. *Northeast Gulf Science.* 7:171-174.

_____ and S.M. RAY. 1985. Relationships between possible available food and the composition, condition and reproductive state of oysters from Galveston Bay, Texas. *Contributions in Marine Science.* 28:109-121.

ST. AMANT, L.S. 1938. Studies on the distribution of the Louisiana oyster drill, *Thais floridana haysae* Clench. Masters Thesis. Louisiana State University, Baton Rouge, Louisiana. 108 pp.

VAN SICKLE, V.R., B.B. BARRETT, T.B. FORD, and L.J. GULICK. 1976. Barataria Basin: salinity changes and oyster distribution. Louisiana Department of Wildlife and Fisheries, Technical Bulletin. 20. 22 pp.

WALNE, P.R. 1970. The seasonal variation of meat and glycogen content of seven populations of oysters *Ostrea edulis* L. and a review of the literature. *Fisheries Investigations, Ministry of Agriculture, Fisheries and Food.* (London, Series 2). 26:1-35.

Contributions in Marine Science. (1989) Vol. 31:95–117.

NEKTON ASSEMBLAGES OF THE CALCASIEU ESTUARY

James D. Felley[1]

Department of Biological and Environmental Sciences
McNeese State University
Lake Charles, Louisiana 70609

ABSTRACT

Nekton was sampled monthly by trawl in Calcasieu Lake, a chenier-plain estuary in southwestern Louisiana, from October 1983 to August 1986. Additionally, nekton was sampled monthly by seine in Calcasieu Lake and in three tributaries of the estuary from September 1985 to August 1986. For each sample, number of individuals and total biomass of each species were recorded and individuals of commercially-important species (penaeid shrimps, *Brevoortia* spp., sciaenids) were weighed and measured. Nekton assemblages of Calcasieu Lake were identified by detrended correspondence analysis (DCA), performed separately on data from trawl samples and from seine samples. Both analyses demonstrated the importance of seasonal changes in species composition in the estuary. Additional patterns in species composition were specific to each data set. DCA of trawl data identified a group of species that was regularly sampled and a group that was sampled sporadically. Analysis of seine samples identified an assemblage characteristic of marshy shorelines and one characteristic of open shorelines.

In all seasons, penaeid shrimps, sciaenids and *Brevoortia patronus* were among the most important forms in the estuary. These species appeared as postlarvae or small juveniles, and grew to adult sizes within the estuary. While in the estuary, several of these species moved into freshwater tributaries of the estuary. These tributaries comprise an important nursery area for many estuarine species.

INTRODUCTION

The Calcasieu Estuary of southwestern Louisiana includes a large lagoon (Calcasieu Lake) and associated waterways. It is a typical "chenier-plain estuary" (Gosselink, Cordes and Parsons 1979). The estuary and adjacent Gulf of Mexico waters are highly productive, accounting for a large proportion of Louisiana's shellfish and finfish resources (NMFS 1986). The Calcasieu estuary is presumably a crucial component in maintaining the commercial fisheries of southwestern Louisiana, but its nekton species are poorly known.

---

[1] Present address: Office of Information Resource Management, Room 2310, A&I Building, Smithsonian Institution, 900 Jefferson Dr. SW, Washington, D.C. 20560

Past research on the nekton of the estuary concentrated on particular marshy areas draining into Calcasieu Lake (Herke, Rogers and Grimes 1984) and on upstream, oligohaline reaches (Felley and Felley 1986; Thompson and Fitzhugh 1986). Some nekton collection sites within the lake were included in a survey of adjacent Gulf of Mexico waters (DeRouen, Hann, Casserly, Giammona and Lascara 1983). The aim of this study was to investigate in detail the nekton fauna of the Calcasieu Estuary, sampling all species assemblages that might interact with the estuary. This study was part of a multidisciplinary survey of the Calcasieu estuarine ecosystem (DeRouen and Stevenson 1987).

This study and Felley (1987a) together define the nekton faunas of the Calcasieu Estuary. Felley (1987a) concentrated on the faunas of waterways (bayous) draining into the estuary, and on the effects of human activities upon various species. The present study identifies the structure of the Calcasieu Lake fauna and the utilization of oligohaline nurseries by early life stages of particular estuarine species (Rozas and Hackney 1983, 1984).

MATERIALS AND METHODS

Monthly samples were taken at locations S1, S2, S4, W, N, and I (Fig. 1) from October 1983 to August 1986 (except from May 1985 through September 1985). Samples were taken at location H from October 1983 to April 1985, but this location could not be sampled in fall 1985 due to low water levels. Sampling at location H was subsequently discontinued. Trawl samples were also taken from other locations in the lake (indicated by unlabelled dots in Fig. 1) at three-month intervals from October 1983 to May 1985. Each trawl sample was taken with a 4.9 m commercial trawl (2.54 cm square mesh) with otter boards (60.5 × 31 cm), towed at 6 km/hr for 10 min. Replicate trawls were taken at each location from October 1983 to April 1985. There were oyster reefs at stations W and I, the substrate at all other locations was soft.

Seine samples were taken from September 1985 through August 1986 from the shoreline adjacent to stations S1, S2, S4, W, N and I. Lengths of the shoreline (6-8 m) were seined with a 9.1 m, 5 mm mesh bag-seine. The substrate was soft at locations S1, S2, S4 and I, and soft sediment mixed with shell at locations W and N. *Spartina alterniflora* grew into the intertidal zone at stations W, S4 and S2. Intertidal zones at other locations were not vegetated. Seine samples were taken from Choupique Bayou, Bayou d'Inde and Contraband Bayou at locations indicated by prefixes of P, D and C, respectively (Fig. 1), from September 1985 through August 1986. The substrates in these bayous were primarily soft. At each bayou location, a flat-seine (3.7 m, 3 mm mesh) was pulled along 5-8 m of shoreline.

Water temperature, dissolved oxygen, pH and conductivity were measured with a series 4000 Hydrolab at all locations. Measurements were taken just above the bottom and just below the surface. Beginning in September 1985, these measurements were also taken at 1-m intervals in the water column.

All nekton were preserved, some in 10% formalin, some packed in ice for other analyses (DeRouen and Stevenson 1987). On occasion, a species was so abundant that a subsample was taken and total numbers and biomass were estimated. Otherwise, all individuals were sorted and identified to species, and total weight of the species in that sample was determined (to 0.1 g). From each sample, up to 25 randomly chosen specimens of commercially important species were individually measured and weighed. Measurements were total length (tip of rostrum to distal end of the telson) for commercial shrimps (*Penaeus* spp.) and standard length for fishes (*Brevoortia* spp. and all sciaenids). Length-frequency distributions were then used to study temporal and spatial occurrences of particular size classes.

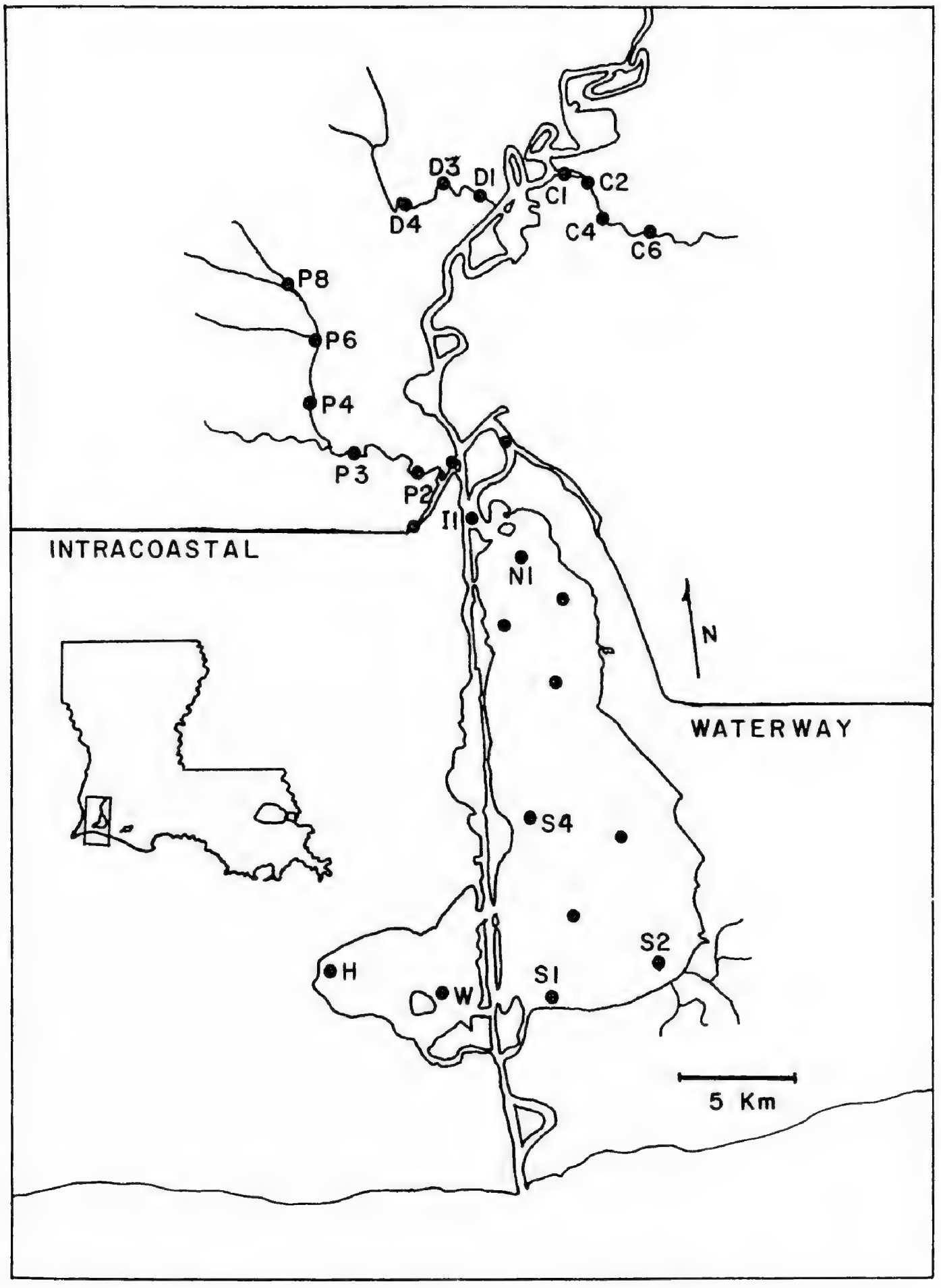


FIG. 1. Map of Calcasieu Estuary, indicating sampling locations. Trawl collections were made monthly or quarterly from locations with prefixes of "I", "N", "W", "H" or "S". From September 1985 to August 1986, seine collections were made from shorelines adjacent to all labelled locations, except for location "H". Trawl collections were made at irregular intervals from unlabelled localities.

The method of detrended correspondence analysis (DCA) was used to identify patterns of variation (temporal or spatial) in species composition of samples. The DECORANA program (Hill 1979) was used to calculate DCA ordinations in this study. DCA yields information on the similarity and differences of particular samples based on the species found in these samples. Gauch (1982) discussed DCA (a form of reciprocal averaging; Hill 1974) and reviewed a number of examples of its use. Kenkel and Orloci (1986) considered DCA to be one of the better metric methods for summarizing community data, though they suggested that no one ordination method can be guaranteed to be appropriate under all circumstances.

The data subjected to DCA are in the form of a species-by-sample matrix. The matrix contains numbers of individuals of each species in each sample. DCA then ordinates (arranges) species according to trends in their occurrence in particular samples and simultaneously ordinates samples according to trends in occurrence of particular species in these samples. For example, DCA might identify species A and B as similar, because they tend to occur in the same samples. Species C and D (which co-occur but are never found with A and B) would be identified as a different set of species. The same analysis would also identify the samples containing A and B as samples from the same species assemblage, and would show that samples containing C and D represent a different assemblage. DCA produces a set of axes, each axis summarizing a separate pattern of variation of species and samples. Both species and samples are represented graphically according to their scores on an axis. Interpretation of community patterns involves inspection of sample and species scores on an axis, and determination of the likely reason why certain species or samples are ordinated close to one another, while others are distant from each other.

Rare species may present a problem in DCA, as the occurrence of a species in only one or two samples may produce a DCA axis that separates only those samples from all the rest. DECORANA allows "down-weighting" of rare species, which reduces their effects on the overall analysis. The down-weighting option was used for this study. Rare species can overly influence DCA results, but their occurrence in particular samples might reflect local conditions of interest (this was found to be the case in the seine-sample data). Thus, rare species were not excluded, but the down-weighting procedure reduced their effects on DCA results.

A separate DCA was run on data for trawl samples and lake seine samples. For each data set, DCA was performed on a matrix containing numbers of all species collected at all locations. In this study, DCA identified community patterns of spatial variation (change in species composition over diverse gradients) and temporal variation (primarily change in species composition over seasons). These trends were interpreted by noting the dates and locations of samples with similar scores, and by inspecting the patterns of species scores on these axes.

RESULTS

Physicochemistry

Waters of Calcasieu Lake are subject to the wide variation in physicochemistry usual in estuaries (Lauff 1967). The lake is shallow and easily mixed by winds, so dissolved oxygen levels tended to be high (usually between 5.0 and 11.0 mg/l, depending on the season, with a yearly mean of 8.2 mg/l) and homogeneous throughout the water column. Pockets of low-oxygen water were occasionally recorded (lowest was 2.2 mg/l), but hypoxia was unusual. Values of pH within Calcasieu Lake were usually between 7.0 and 8.3 (range 6.2 - 9.1, mean 7.6).

Temperature and salinity were highly variable in the Calcasieu Estuary, reflecting patterns of freshwater inflow and saltwater exchange with the Gulf of Mexico. Figures 2 and 3 illustrate seasonal variation in temperature and salinity for the north and south ends of Calcasieu Lake (north-end stations

included N and I, south-end stations were those with prefixes of S, W, or H; Fig. 1). Monthly data summarized in the figures were collected from one or more years, and from two to eight locations at the north end, and four to eight locations at the south end. Thus, the standard-error bars about each monthly mean reflect both variation among locations in a year and variation over years.

Temperature ranged from 6.0 to 31.0°C over the study period. Wide variation between north- and south-end locations was evident from January to March (Fig. 2), reflecting inflow of cool freshwater in these months. From April to May, temperatures increased steadily throughout the lake. Temperatures were high from June to August, began dropping in September, and dropped steadily from October to December.

Salinity was widely variable in the lake, but was consistently lower in the north end, due to the input of freshwater from the Calcasieu River and bayous that drained upland watersheds. The rainy season (usually December through May, according to Geraghty, Miller, Van der Leeden and Troise 1973) produced a decline in salinity at the north end of the lake that was especially apparent from December through April (Fig. 3). Throughout the lake, salinity was highest from July through September, when rainfall over the Calcasieu drainage and estuary was local and intermittent.

Patterns of variation in salinity and temperature are summarized in Fig. 4, which presents coefficients of variation for these variables. The variation illustrated in Fig. 4 subsumes variation between years, between the two ends of the lake, and between stations within each end. Thus, Fig. 4 illustrates the

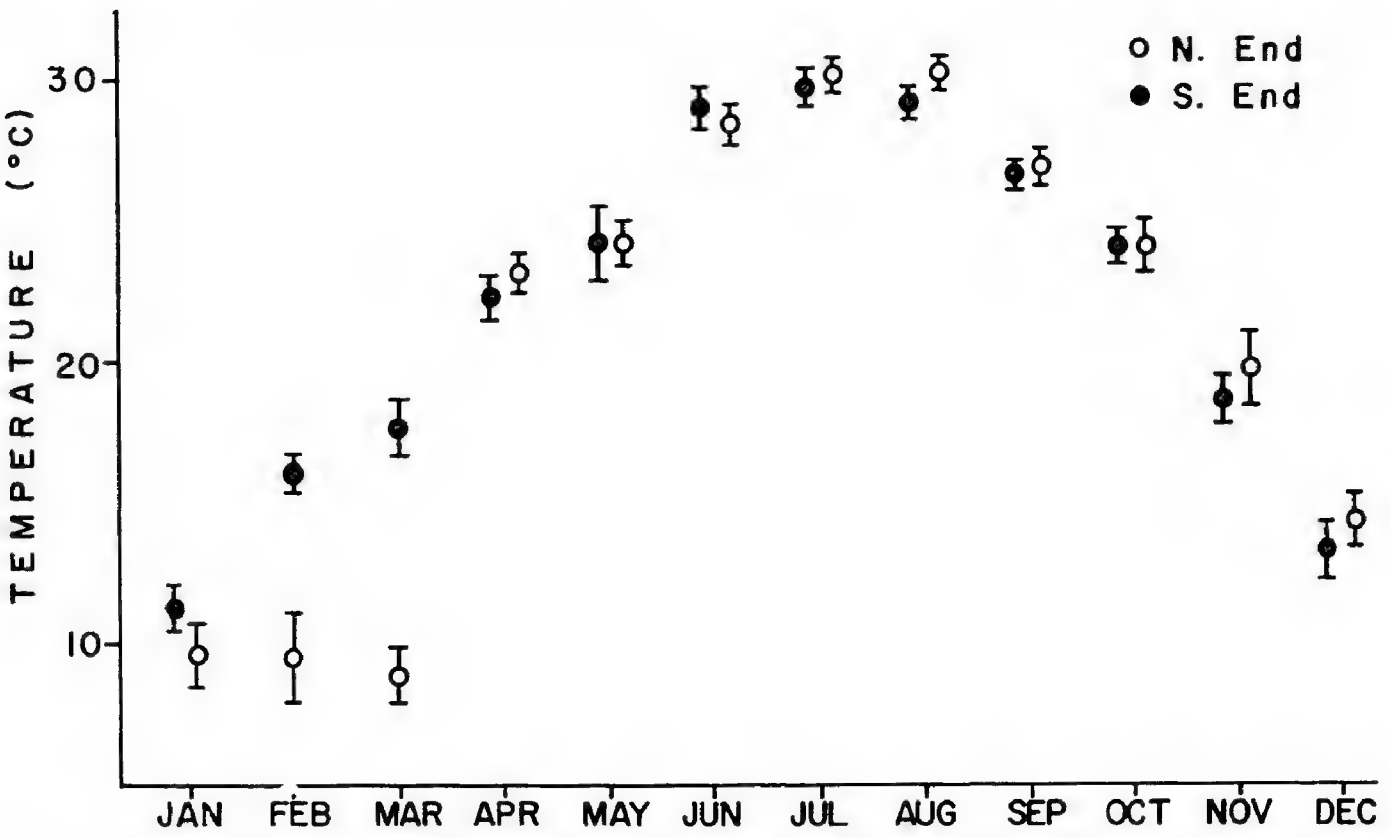


FIG. 2. Temperature variation in Calcasieu Lake. North-end stations had prefixes of "I" or "N"; south-end stations had prefixes of "H", "W" or "S" (Fig. 1). Circles represent monthly means from 1983 to 1986, bars represent 2 standard errors about the mean.

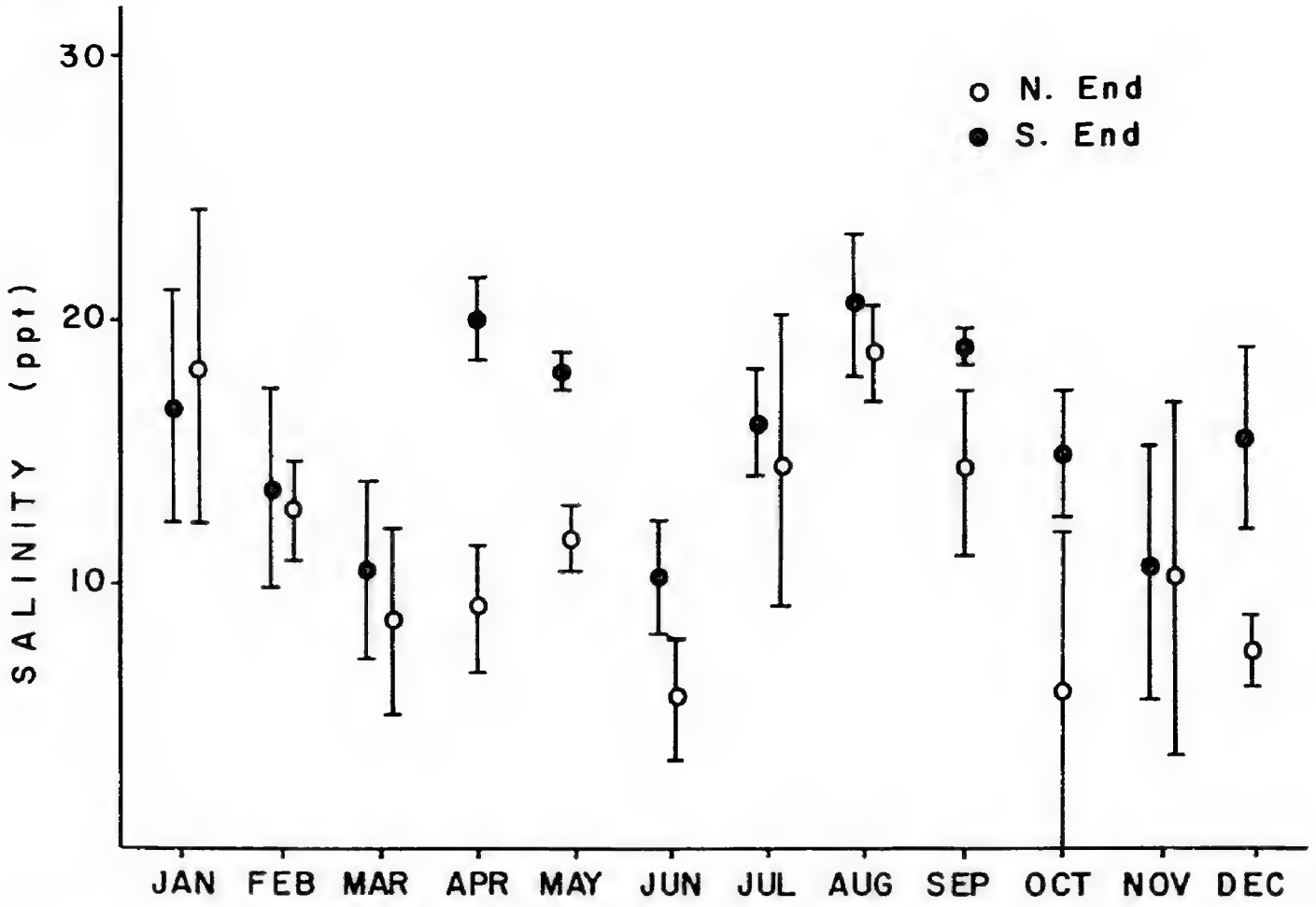


FIG 3. Salinity variation in Calcasieu Lake. North-end stations had prefixes of "I" or "N"; south-end stations had prefixes of "H", "W", or "S" (Fig. 1). Circles represent monthly means from 1983 to 1986, bars represent 2 standard errors about the mean.

variation in conditions to which a species might be exposed at any time in Calcasieu Lake. Variation was high for both variables from January to March, tended to decrease from April through June, was low from July through September, and rose dramatically from October through December.

Seasonal variation in the lake's physicochemistry can be summarized as follows:

In winter (January-March), temperatures and salinities were low and quite variable.

Spring (April-June) was characterized by rising and less variable temperatures and salinities.

Summer (July-September) was a season of high temperatures and salinities, with little variation.

Fall (October-December) was characterized by declining and variable temperatures, and highly variable salinities.

In terms of physicochemistry, the estuary was most predictable in summer and least predictable in fall and winter.

The three bayous feeding the upper estuary were estuarine in their lower portions and freshwater in their upper portions. Physicochemistry of the three bayous was differentially affected by human impacts. Bayou d'Inde receives municipal and industrial wastes. Contraband Bayou receives municipal wastes, and Choupique Bayou does not receive either municipal or

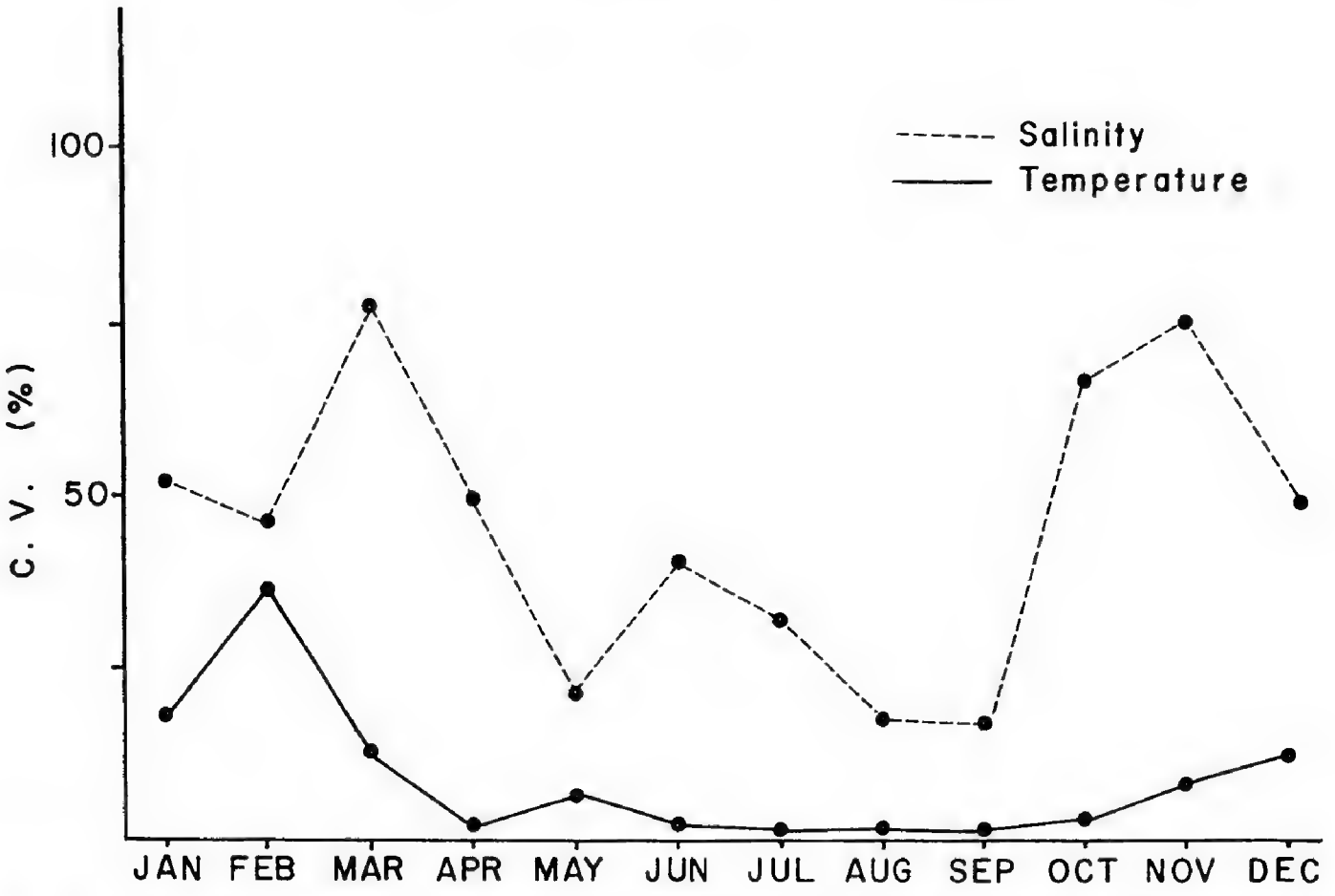


FIG. 4. Coefficients of variation (C.V.) for temperature and salinity in Calcasieu Lake. Each point represents the coefficient of variation calculated for a month, over all localities within the lake and all years.

industrial wastes. Felley (1987a) details the physicochemistry of these bayous, and associated human impacts.

Nekton Assemblages

A total of 121 species of nekton (macroinvertebrates and fishes) were found within the Calcasieu Estuary and associated waterways. Of these, 34 were typically freshwater forms, considered in detail by Felley (1987a) in an analysis of bayou nekton assemblages. Raw data for all collections is given in DeRouen and Stevenson (1987). The most regularly-occurring species of Calcasieu Lake are included in Tables 1 and 2. Gosselink *et al.* (1979) provide a referenced outline of life-history, foods, and habitat preferences of nekton species of the Calcasieu Estuary and other chenier-plain estuaries. Information on biology of particular species discussed here can also be found in Kilby (1955), Simpson and Gunter (1956) and Hoese and Moore (1977).

Trawl Data

A total of 296 trawls were taken from October 1983 to August 1986. The most frequently occurring forms (taken in over 50% of trawls in all seasons) were *Callinectes sapidus, B. patronus, Leiostomus xanthurus* and *Micropogonias*

TABLE 1

Nekton species found in trawl samples from Calcasieu Lake, by season. Samples were taken from October 1983 to August 1986 (see text for details of dates and trawling methods). Number of samples is given in parentheses. Given under each season is the percentage of trawls in which a species occurred, abbreviated as "Fq" (frequency), and the average number of individuals sampled per hour of trawling (under "Num"). Abbreviations following species' names correspond to those in Fig. 5.

Species	Winter (109)		Spring (64)		Summer (42)		Fall (81)	
	Fq	Num	Fq	Num	Fq	Num	Fq	Num
Molluscs								
Lolliguncula brevis (LOLL)	2	0.1	14	2.2	10	1.0	4	0.2
Decapods								
Penaeus aztecus (PENA)	22	3.7	62	155.7	38	17.1	38	11.2
P. setiferus (PENS)	39	22.4	81	88.6	93	446.9	95	358.1
Callinectes sapidus (CALL)	81	60.8	95	102.8	81	21.8	84	33.0
Fishes								
Brevoortia patronus	53	25.5	94	70.7	55	12.1	54	53.9
Dorosoma cepedianum	11	0.8	5	0.3	10	0.9	11	0.9
Anchoa mitchilli (AMIT)	24	5.1	33	6.1	24	17.9	36	14.4
Ictalurus furcatus (IFUR)	--	--	--	--	--	--	1	0.1
Arius felis (AFEL)	10	1.2	34	12.9	43	18.6	22	11.0
Urophysis floridana (UFLO)	5	0.3	5	0.3	--	--	--	--
Prionotus tribulus	3	0.2	16	2.1	--	--	7	3.0
Caranx hippos (CHIP)	--	--	--	--	12	1.9	--	--
Archosargus probatocephalus (APRO)	13	1.6	3	0.2	2	0.3	2	0.1
Cynoscion arenarius (CARE)	5	0.3	37	8.0	52	18.7	63	19.0
C. nebulosus (CNEB)	13	1.0	3	0.3	2	0.1	20	2.4
Leiostomus xanthurus (LXAN)	61	21.6	67	27.1	57	26.0	74	32.7
Micropogonias undulatus (MUD)	72	29.3	95	123.4	86	59.3	90	32.2
Pogonias cromis (PCRO)	26	4.2	9	1.1	14	1.0	30	6.1
Sciaenops ocellatus (SOCE)	1	--	3	0.2	--	--	--	--
Chaetodipterus faber (CFAB)	1	--	9	0.6	26	7.3	7	1.5
Mugil cephalus (MCEP)	41	19.5	8	0.8	5	0.4	20	8.0
Trichiurus lepturus (TLEP)	5	0.7	22	7.3	7	0.4	5	0.4
Peprilus alepidotus	--	--	3	0.2	12	2.1	1	--
P. burti	12	5.0	28	8.0	10	1.0	2	0.2
Citharichthys spilopterus (CSPI)	8	1.7	20	2.6	71	18.1	28	9.5
Etropus crossotus (ECRO)	1	--	6	0.4	33	6.8	17	3.1
Paralichthys lethostigma (PLET)	9	0.9	23	2.7	29	2.7	11	1.2

undulatus (Table 1). *Penaeus setiferus* was a frequently occurring species in all seasons but winter, and *Penaeus aztecus* was a frequently occurring species in spring. In summer and fall, *Cynoscion arenarius* was found in more than 50% of trawls.

DCA produced three axes that summarized variation in species occurrence and abundance. The first axis contrasted all other samples with a sample containing only *Hemicaranx amblyrhynchus*. Axis 2 summarized seasonal variation in species occurrence and axis 3 differentiated certain species that

TABLE 2

Nekton species found in seine samples taken in Calcasieu Lake, September 1985 to August 1986. Number of samples is given in parentheses. Percentage of samples in which a species occurred is given under "Fq" (frequency), while average number per sample is given under "Num". Abbreviations following species names correspond to those in Fig. 6.

Species	Winter (16)		Spring (13)		Summer (15)		Fall (14)	
	Fq	Num	Fq	Num	Fq	Num	Fq	Num
Decapods								
Penaeus aztecus (PENA)	--	--	94	29.7	60	7.0	57	6.5
P. setiferus (PENS)	37	3.8	41	107.5	87	29.4	64	14.7
Palaemonetes intermedius	30	24.2	23	0.4	20	0.3	--	--
P. pugio (PALP)	93	148.7	82	53.3	67	74.3	71	63.0
P. vulgaris	56	5.6	11	0.3	--	--	79	6.7
Callinectes sapidus (CALL)	63	12.5	35	0.8	67	3.5	50	2.3
Fishes								
Elops saurus	--	--	11	0.1	7	0.1	--	--
Alosa chrysochloris (ACHR)	--	--	11	0.1	20	0.3	--	--
Brevoortia patronus (BPAT)	100	1168.0	94	533.7	40	14.1	36	2.6
Anchoa hepsetus	--	--	11	1.7	13	1.3	14	0.1
A. mitchilli (AMIT)	50	12.5	76	231.9	87	59.1	79	31.5
Arius felis (AFEL)	--	--	6	0.2	33	0.8	--	--
Cyprinodon variegatus (CVAR)	25	0.3	6	0.1	--	--	29	0.8
Fundulus grandis (FGRA)	50	1.6	11	0.3	33	0.7	21	0.5
F. similis (FSIM)	7	0.2	--	--	20	0.2	14	0.2
Poecilia latipinna	--	--	--	--	7	0.1	14	0.2
Membras martinica (MMAR)	12	0.2	35	2.8	73	5.5	29	1.8
Menidia beryllina (MEND)	93	46.9	71	9.4	53	4.4	57	18.5
Syngnathus louisianae (SLOU)	7	0.1	11	0.1	7	0.1	--	--
Oligoplites saurus (OSAU)	--	--	--	--	40	1.7	--	--
Lagodon rhomboides (LRHO)	32	3.6	23	0.2	27	0.4	--	--
Bairdiella chrysoura (BCHR)	--	--	11	1.1	26	3.4	--	--
Cynoscion arenarius (CARE)	--	--	29	2.4	46	6.4	14	0.2
Leiostomus xanthurus (LXAN)	37	25.1	23	2.3	--	--	14	0.2
Micropogonias undulatus (MUND)	100	299.9	64	8.9	33	0.6	64	28.0
Mugil cephalus (MCEP)	37	6.8	23	0.9	33	1.5	29	0.6
M. curema (MCUR)	--	--	17	18.3	26	1.3	--	--
Gobionellus boleosoma (GBOL)	6	0.1	6	0.1	20	0.2	29	0.9
Gobiosoma bosci (GBOS)	37	0.8	6	0.1	--	--	36	0.6
Sphoeroides parvus	--	--	6	0.1	13	0.1	--	--

occurred irregularly (*i.e.*, sporadically in small or large numbers) from the more commonly-collected species. Fig. 5 illustrates species scores on axes 2 and 3. Abbreviations for species are in Table 1; note that not all species listed in Table 1 are illustrated in Fig. 5.

A particular seasonal assemblage was most easily characterized by those species that appeared in abundance only in that season. For example, the winter assemblage included *Archosargus probatocephalus* and *Mugil cephalus*, two species that were commonly taken in winter, but were either

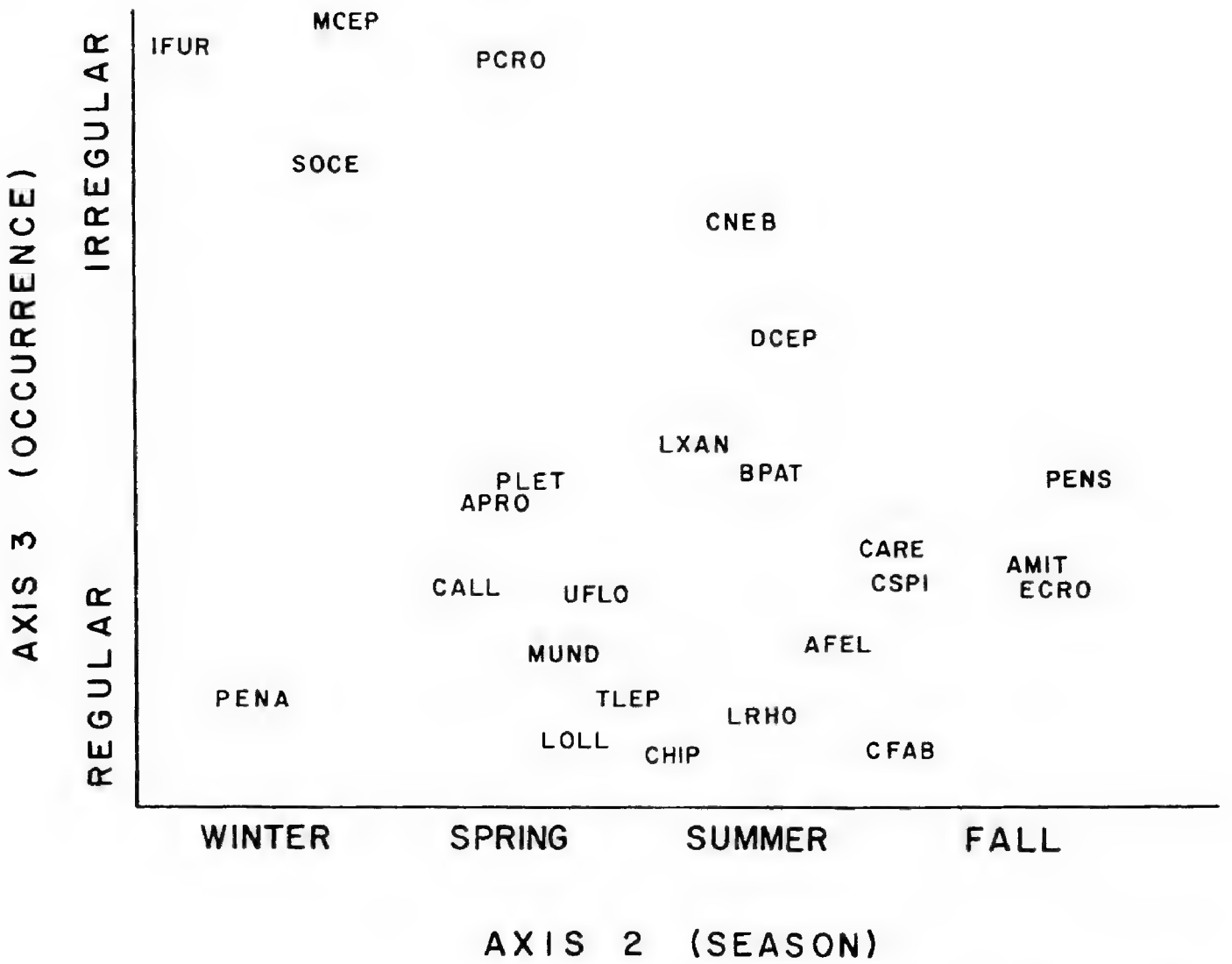


FIG. 5. Detrended correspondence analysis (DCA) of nekton species from trawl samples within the Calcasieu Lake. Axis 1 differentiated one sample from all others, and is not illustrated. Axis 2 represented seasonal variation in nekton assemblages. Axis 3 differentiated species of regular occurrence from those that were of irregular occurrence and whose capture reflected special or unusual conditions at that locality and time. Abbreviations are given in Table 1.

absent or were taken infrequently in other seasons (Table 1). The winter fauna also included some rarely caught freshwater forms taken in the upper lake near the mouths of bayous, such as *Ictalurus furcatus* (taken in December, Table 1) and *Lepomis macrochirus*. The spring assemblage was identifiable by the appearance of such characteristic species as *Lolliguncula brevis, P. aztecus, Urophysis floridana, Prionotus tribulus, Trichiurus lepturus, Peprilus burti* and *Paralichthys lethostigma*. Some of these species (notably *P. aztecus*) could be found in winter or summer, but were most abundant in spring. Common summer species were *Arius felis, Caranx hippos, Lagodon rhomboides, C. arenarius, Chaetodipterus faber, Peprilus alepidotus* and *Etropus crossotus*. There were no species that appeared exclusively in fall. The seasonal faunas merged in some months. In March (the last month of "winter"), a number of characteristic spring season forms began appearing in the lake, such as *L. brevis* and *T. lepturus*. Also, some members of the winter fauna were found regularly in December (*Cynoscion nebulosus*, and *M. cephalus*, in particular). A species' score on axis 2 tended to reflect the season in which it formed an important part of the nekton assemblage. Exceptions

included *P. aztecus* (most abundant in spring, but grouped with winter species), *A. probatocephalus* (most common in winter, but grouped with spring species), and *E. crossotus* (most common in summer, but grouped with fall species).

Some species were found in relatively high numbers in all seasons (Table 1) and were part of any season's characteristic assemblage. These included *P. setiferus, C. sapidus, B. patronus, Anchoa mitchilli, L. xanthurus, M. undulatus, Pogonias cromis* and *Citharichthys spilopterus*. In general, these species' scores on axis 2 identified them with the season in which they were most abundant. An exception was *B. patronus*, which was most common in spring but was grouped with summer species. The fall assemblage (for which no characteristic species could be identified) included some commonly-occurring species that had peaks of abundance in this season (*e.g., P. setiferus* and *A. mitchilli*).

The third DCA axis differentiated the commonly-caught species from a diverse group of species that were caught only under special conditions. The latter were termed species of irregular occurrence (as they were either taken in small numbers, or they occurred sporadically in relatively high numbers). Species commonly found in a season's trawl samples tended to have low scores on this axis. Irregularly-occurring species with high scores included *Dorosoma cepedianum, I. furcatus, C. nebulosus, P. cromis, Sciaenops ocellatus* and *M. cephalus* (Fig. 5). Appearance of these species in a particular trawl was linked to special and localized conditions associated with the sampling site. For example, *I. furcatus* and *D. cepedianum* are freshwater forms that were found at locations where salinity was low. *Pogonias cromis* was mostly taken in trawls which passed directly over oyster reefs. *Sciaenops ocellatus, C. nebulosus* and *M. cephalus* are very active forms that can easily evade a trawl (*Mugil* sp., in particular, could often be seen jumping over the trawl). These species only appeared in trawls taken in very cold conditions (when these forms may have been swimming too slowly to evade the trawl) or during very turbid conditions (when they may not have realized they were within the trawl). DCA grouped all of the above as species that were not found with the "normal" assemblage of a season.

Patterns of species abundances and occurrences were relatively constant over the course of this study. No yearly differences were apparent in overall species composition (as judged by DCA). However, there were some differences in particular species' abundances from one year to another (data in Felley 1987b). For example, fall 1983 (when the study was initiated) was characterized by higher numbers of *L. rhomboides* and lower numbers of *D. cepedianum* than the other two years. In winter 1985, there were more *P. aztecus* and *P. setiferus* than in 1984 or 1986, whereas in spring 1986 more flatfishes were taken than in 1985.

Seine Data

Table 2 lists seasonal occurrences and average numbers of species collected by seine. Frequently occurring species were those found in more than

50% of the samples over the whole year or in a particular season. Species occurring frequently in all seasons were *Palaemonetes pugio, C. sapidus, A. mitchilli* and *Menidia beryllina*. Species frequently taken in winter were the species listed above, as well as *B. patronus* (which was also commonly found in spring), *Fundulus grandis* and *M. undulatus*. Frequently occurring species of other seasons were *P. aztecus* (spring), *P. setiferus* (summer and fall), and *Palaemonetes vulgaris* (fall and winter).

Sample data were subjected to DCA, which produced three interpretable axes. Axis 1 distinguished one sample from the rest. In October 1985, the sample from station S4 (Fig. 1) contained three species that were either never found again in the lake (*Larimus fasciatus*) or that were rarely found at other times but were very abundant in this collection (*Acetes americanus* and *Xiphopenaeus kroyeri*). Some local condition affecting only this site may have accounted for the occurrence of these species. This axis was not interpreted further. Axes 2 and 3 identified nekton assemblages associated with particular seasons (axis 2) or particular types of shorelines (axis 3) (Fig. 6).

Seasonal variation in species composition was pronounced (Table 2). Some species were found throughout the year. These species' DCA scores tended to

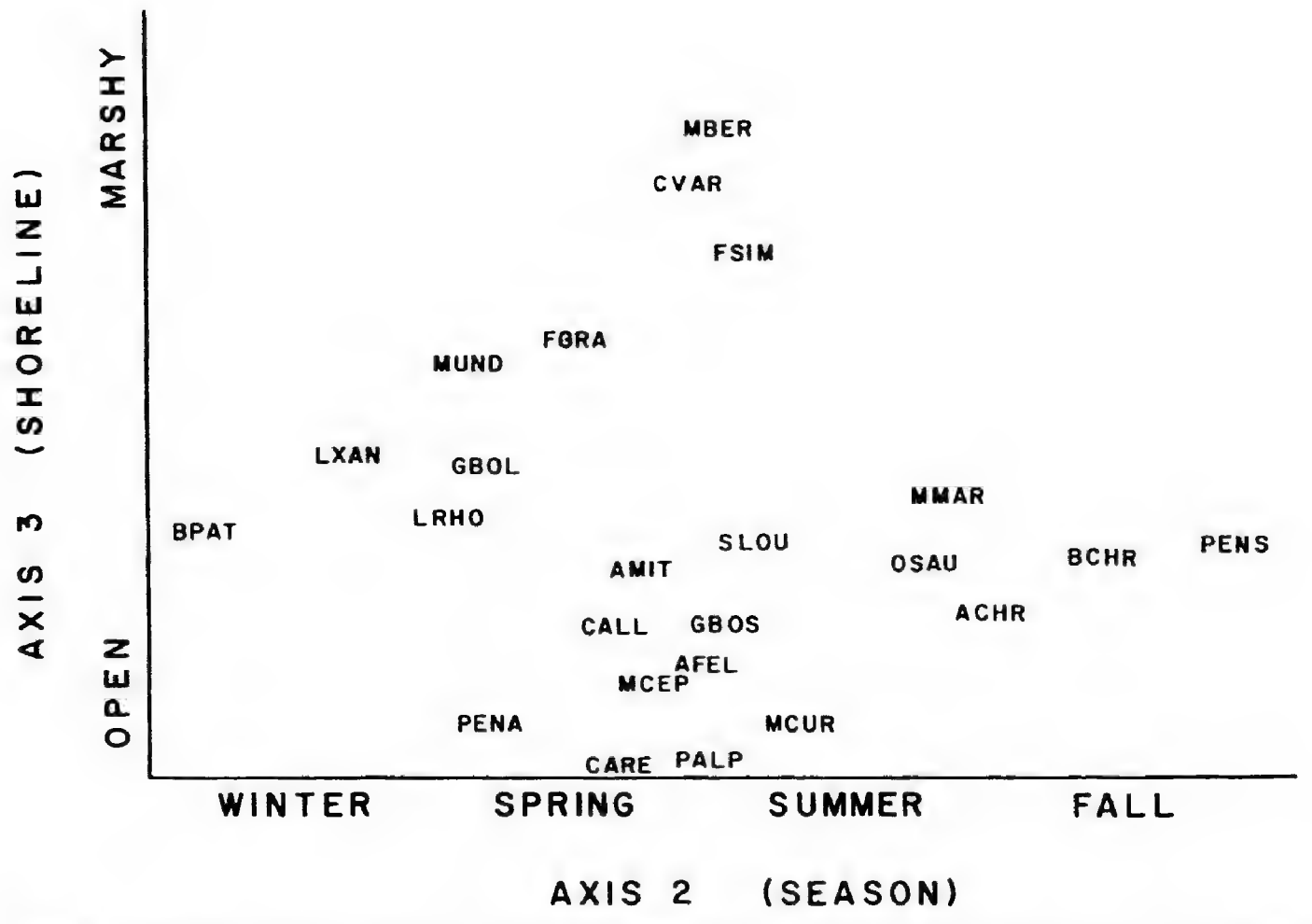


FIG. 6. Detrended correspondence analysis (DCA) of nekton species from seine samples within Calcasieu Lake. Axis 1 differentiated one sample from all others, and is not illustrated. Axis 2 reflected seasonal variation in nekton assemblage structure. Axis 3 differentiated species on the basis of type of shoreline where they were most common. Open shoreline had little cover and/or relatively high wave action. Marshy shorelines had much cover provided by *Spartina alterniflora* growing in the water, and had relatively low wave action. Abbreviations are given in Table 2.

group them with the seasonal assemblages in which they were most abundant (Fig. 6). For example, *P. pugio, B. patronus, F. grandis*, and *M. undulatus* had scores identifying them with the winter assemblage, while *P. setiferus, A. mitchilli* and *Membras martinica* had scores reflecting their importance in summer and fall assemblages. Other species were only found in the lake in certain seasons. Among the shore shrimps, *P. vulgaris* was found in fall and winter, *Palaemonetes intermedius* primarily in winter and spring. Both species were much less common than *P. pugio*, the dominant shore shrimp in the lake. A large number of species appeared in the lake in spring and summer, including *Elops saurus, Alosa chrysochloris, A. felis, Oligoplites saurus, Bairdiella chrysoura* and *Sphoeroides parvus*. Gobies (primarily *Gobionellus boleosoma* and *Gobiosoma bosci*) were most common in fall and winter. These trends are reflected in species scores (Fig. 6) and species frequencies and densities (Table 2).

Axis 3 contrasted samples at two stations (W and S2) with those taken elsewhere. These localities had higher numbers of cyprinodontids (including *Cyprinodon variegatus, F. grandis* and *Fundulus similis*) as well as of *M. beryllina* (Fig. 6). These species seemed to be associated with low-energy shorelines where vegetation grew into the water. Actively swimming forms such as *Mugil* spp., *B. patronus, A. mitchilli* and *C. arenarius* tended to be found on open shorelines where wave-action could be relatively high.

Life History of Individual Species

Months of occurrence and spatial distribution were investigated for particular size classes of commercial shrimps, menhaden, and several drum species. For each species, four size-ranges were identified, corresponding generally to the following age classes: youngest recruits to the estuary, small juveniles, large juveniles, and adults.

Commercial shrimp (*Penaeus* spp.) size-groups (and corresponding age classes) were as follows:

15-25 mm total length (earliest postlarval recruits to the estuary);
26-55 mm (small juveniles, representing young recruits of the year);
56-80 mm total length (large juveniles, representing older recruits of that year);
81 + mm (adults).

These groups were derived from information in George (1962), Baxter and Renfro (1967) and Gaidry and White (1973). In winter and early spring, individuals of sizes 56-80 mm probably represented small overwintering individuals. Seine samples contained postlarvae and both juvenile classes, trawl samples primarily included large juveniles and adults. Gaidry and White (1973) felt that large juveniles and adults represented individuals ready to leave the estuary.

The brown shrimp (*P. aztecus*) was typically a spring and summer species. Adults first appeared in March (water temperatures > 17°C), postlarvae in April (water temperatures > 20°C). Postlarval and small-juvenile recruits

appeared irregularly from April through November, with highest numbers appearing from April through June. April through June was a period of peak abundance for *P. Aztecus* in both trawl and seine samples (Tables 1 and 2). Growth and numbers were high in this period, with spring recruits growing to 60-80 mm by June. Generally, numbers per sample dropped dramatically after July. In spring, *P. aztecus* was found throughout Calcasieu Lake and in the estuarine portions of the bayous (in salinities > 2-3‰, dissolved oxygen levels > 4.0 mg/l). After June, *P. aztecus* appeared only sporadically in the bayous. This species was not found in the freshwater portions of the bayous. These patterns of recruitment, abundance and distribution correspond to those reported in other studies of *P. aztecus* (Gaidry and White 1973; George 1962; Herke *et al.* 1984; St. Amant, Broom and Ford 1966).

The white shrimp (*P. setiferus*) was found in the estuary throughout the year (Table 3) and in summer and fall appeared throughout the estuary and into freshwater tributaries. This species was abundant in the estuary from spring through fall (Tables 1, 2; Felley 1987a). Adults and large juveniles occurred in low numbers in trawl samples from January and February, and began appearing in abundance in March. Recruitment of postlarvae occurred intermittently from spring through fall, with peaks in March-April (lake temperature 17-20°C) and in June-July. Postlarvae were found throughout the lake and in the estuarine portions of the bayous. From July to October, juveniles were found in the most upstream portions of the bayous (Table 3), often in large numbers (Felley 1987a). In the freshwater reaches, individuals occurred in water with conductivity as low as 0.14 mmhos/cm, and with dissolved oxygen as low as 2.5 mg/l. Williams (1955) noted that small *P. setiferus* preferred salinities less than 10‰, and Renaud (1986) showed that *P. setiferus* was less sensitive to low oxygen levels than *P. aztecus*. Other studies of the estuarine cycle of *P. setiferus* (Baxter and Renfro 1967; Gaidry and White 1973; Herke *et al.* 1984) have shown patterns of recruitment, abundance and distribution similar to those found here.

Gulf menhaden (*Brevoortia patronus*) was an important component of the estuarine assemblage. All individuals identifiable to species (*i.e.*, juveniles and adults) were *B. patronus*. *Brevoortia gunteri* is found in the northwestern Gulf of Mexico (Hoese and Moore 1977) but was at best a rare and minor constituent of the Calcasieu Estuary fauna. Size classes and corresponding life-history stages, derived from information in Jones, Martin and Hardy (1978), Lassuy (1983) and Nelson and Ahrenholz (1986), were as follows: 10-30 mm (larvae), 31-59 mm (small juveniles), 61-100 mm (large juveniles), 100+ mm (adults). Larvae and small juveniles were collected primarily by seine, large juveniles and adults primarily by trawl.

Brevoortia patronus occurred in the estuary in all months of the year. Recruitment of larvae occurred from November through July (Table 3), with highest numbers of larvae occurring from January through June. This size-class was typically found throughout the estuary and well into freshwater reaches of the bayous. While early life-stages were abundant in the freshwater reaches, utilization of these areas declined as individuals grew. Small

TABLE 3

Seasonal and spatial distribution of size-classes of some commercially important species of the Calcasieu Estuary. For each species and size-class, "X" indicates occurrence in Calcasieu Lake, "X+" occurrence in Calcasieu Lake and estuarine portions of tributaries, "X++" occurrence in Calcasieu Lake and in both estuarine and freshwater portions of such tributaries.

Species / Size (mm)*	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Penaeus aztecus												
15-25				X	X+	X+						
26-55				X+	X+	X+	X		X+	X+	X	
56-80			X	X	X+	X+	X+		X	X	X	X
81+			X	X	X	X	X	X	X	X	X	X
Penaeus setiferus												
15-25			X+	X+		X+	X+	X	X+		X	X+
26-55		X			X	X	X+	X+	X++	X++	X	X
56-80	X	X	X		X	X	X++	X+	X++	X++	X	X
81+	X	X	X	X	X	X	X	X	X++	X	X	X
Brevoortia patronus												
10-30	X+	X++	X++	X++	X++	X++	X++				X	X++
31-60		X	X	X	X+	X++	X++	X+	X+			
61-100	X		X	X	X	X	X	X	X	X	X	X
100+	X	X	X	X	X	X				X	X	X
Cynoscion arenarius												
10-30				X			X					
31-60				X	X	X	X		X+	X	X	
61-100		X	X	X	X	X	X	X	X	X	X	X
100+			X	X	X	X	X	X		X		X
Leiostomus xanthurus												
20-30			X+	X++	X++							
31-60		X	X+	X++	X++	X++						
61-100	X			X+	X++	X	X+	X	X+	X	X	X
100+	X	X	X	X	X	X	X	X	X	X	X	X
Micropogonias undulatus												
10-20	X+	X+	X++	X++						X	X	X+
21-50	X	X++	X++	X++	X++	X				X	X	X+
51-100	X	X	X	X++	X	X+	X	X	X+			X
100+	X	X	X	X	X	X	X	X	X	X	X	X

* Measurements are total length for *Penaeus* spp., standard length for fishes.

juveniles appeared in collections from Calcasieu Lake from February through August, but did not enter the bayous until May. Large juveniles and adults did not enter the bayous (it is unlikely that they were present there but never sampled). Large juveniles were found in every season in Calcasieu Lake (Table 3), while adults appeared in the lake in fall, winter and spring. Larvae recruiting to the estuary in winter apparently grew into the adult size-class by fall.

Cynoscion arenarius was typically a summer-fall species in the Calcasieu Estuary (Table 3). It could be found in the estuary in all seasons, but was most abundant from spring through fall (Table 1, 2). This species was primarily confined to Calcasieu Lake and was only rarely found in the estuarine portions of bayous that feed the lake (Table 3). Size categories (and associated

life-history stages), derived from information in Shlossman and Chittenden (1981), were as follows: 10-30 mm (earliest postlarval recruits); 31-60 mm (small juveniles); 61-100 mm (large juveniles); 100+ mm (adults). The two smallest size categories were collected mostly by seine and had peak abundances in spring and summer (Table 2). Large juveniles were found year-round in trawl samples, while adults were found in trawl samples from spring through fall (Table 3). These larger size classes had peak densities in summer and fall (Table 1). Apparently, most juveniles and adults moved into the Gulf of Mexico in winter and spring, a movement pattern reported in an Atlantic coastal estuary by Vetter (1982). Shlossman and Chittenden (1981) investigated life-history of *C. arenarius*, finding patterns of recruitment and movement similar to those reported here.

Leiostomus xanthurus was ubiquitous in the Calcasieu Estuary. Size classes and associated life-history stages, derived from information in Johnson (1978) and Kobylinski and Sheridan (1979), were as follows: 20-30 mm (postlarvae), 31-60 mm (small juveniles), 61-100 mm (large juveniles), 100+ mm (adults). The two smallest size classes appeared mostly in seine samples, large juveniles in both seine and trawl samples, and adults primarily in trawl samples. In the Calcasieu Estuary, earliest recruits and small juveniles appeared in large numbers from late winter to spring (Table 2, 3), corresponding to dates in Parker (1971) for recruitment to Texas bays. Within a month of entering the estuary, postlarvae and small juveniles could be found in the freshwater reaches of the bayous. Individuals were found in the bayous until early summer (Table 3), and left as they grew to large-juvenile sizes. From late spring through winter, large juveniles could be found in seine and trawl samples from Calcasieu Lake. Adults were found year-round within Calcasieu Lake, but apparently did not use the bayous to any extent. Postlarvae entering the estuary in winter grew to the 100+ mm size-class by fall (Table 3).

Micropogonias undulatus was another ubiquitous species in the Calcasieu Estuary. Size classes and corresponding life-history stages (derived from information in Johnson 1978) were as follows: 10-20 mm (postlarvae), 21-50 mm (small juveniles), 51-100 mm (large juveniles), 100+ mm (adults). Postlarvae and small juveniles were taken mostly in seine samples, large juveniles in both seine and trawl samples, and adults almost exclusively in trawl samples. Postlarval recruits began appearing in fall (Table 3), with peak abundance of smaller individuals in winter and spring (Table 2). These individuals grew to the adult size-class by fall. Peak abundance of *M. undulatus* in trawl samples was in summer and fall (Table 1). Postlarvae and small juveniles exploited the entire estuary and freshwater areas that feed into the estuary (Table 3). By summer, recruits had grown to large-juvenile sizes and were leaving the bayous. Adults were taken only in Calcasieu Lake. Life-history summaries of *M. undulatus* in the Gulf of Mexico are provided by Kobylinski and Sheridan (1979) and Ward, Armstrong and The Matagorda Bay Project Teams (1980). Life-history of *M. undulatus* in Calcasieu Estuary is a bit different from that presented by Ward *et al.* (1980) for this species in

Matagorda Bay (where *M. undulatus* is apparently much less abundant than it is in the Calcasieu Estuary). They reported that juveniles left the bays for the Gulf of Mexico in July, while the Calcasieu Estuary juveniles were abundant until fall.

DISCUSSION

Analysis of nekton assemblages of the Calcasieu Estuary allowed identification of species groups associated with different seasons and with local environmental conditions. Each assemblage identified by DCA was comprised of species that were ecologically similar, in terms of their temporal or spatial occupation of the estuary. The structure of these assemblages seemed stable from year to year. Trawl data showed that absolute abundances of a particular species may differ from one year to another, and a rare species might appear in low numbers in one year and be totally absent in another. However, the trawl data-set strongly suggests that the structure of the Calcasieu Estuary nekton-assemblage does not change dramatically from one year to the next. The common species of one year are the common species of the next, and species rare in one year are likely to be rare the next. Thus the assemblages identified by both data sets are likely to be characteristic of the Calcasieu Estuary in any year.

There are important ecological differences among the species of each assemblage, differences that were not revealed by this analysis. In fact, the members of an assemblage can include species that use the estuary in very diverse ways—seasonal visitors, residents, forms using the estuary as adults or as juveniles. This diversity of utilization patterns is related to the species' differing life-histories. Insight into why certain species tend to co-occur in collections may be gained by classifying species by the manner in which they use the estuary.

McHugh (1967) suggested classifying nekton species according to the importance of the estuary in the species' life-cycle (his classification was used by Felley (1987b), and a modified version by Thompson and Fitzhugh (1986), to categorize species of the Calcasieu Estuary). McHugh identified the following groups:

(A) marine species which may spend their entire life-cycle outside the estuary, but which appear irregularly in the estuary;

(B) marine species that spawn and spend much of their life-cycle outside the estuary, but use the estuary as a nursery area (adults may visit the estuary on a regular or irregular basis);

(C) marine species which pay regular visits to the estuary, usually as adults;

(D) anadromous and catadromous species;

(E) truly-estuarine species, which complete their entire life-cycle within the estuary; and

(F) freshwater species.

McHugh's category A (marine species appearing irregularly in the estuary) included a number of forms normally found in inshore areas. Examples of

such species collected in seine samples were *Opisthonema oglinum, Sardinella aurita, Anchoa hepsetus, Lutjanus griseus*, and the three species which accounted for axis 1 of the DCA of seine samples. Examples among species collected by trawl were *Synodus foetens, Centropristis philadelphica* and *Pomatomus saltatrix*. Members of this category appeared in low frequencies, and were generally seen in summer and fall. They appeared when Calcasieu Lake most resembled the Gulf of Mexico (*i.e.*, when temperatures and salinities were highest, and physicochemical variability was lowest).

Category B (offshore-spawning species that use the estuary as a nursery) included some of the most important components of the lake's nekton. Examples were penaeid shrimps, sciaenids, *B. patronus* and many other species (see Felley 1987b). Members of this category recruited to the estuary on different schedules. Juveniles of fall-winter spawners appeared in seine samples from fall through spring (*B. patronus, M. undulatus, L. rhomboides, M. cephalus*). Juvenile *P. aztecus* and *L. xanthurus* appeared in spring, as did *C. spilopterus* and *P. lethostigma*. Species that first appeared as postlarvae or juveniles in summer and fall included *P. setiferus, A. mitchilli, C. arenarius* and *C. faber*. Many of these species utilized the freshwater areas of the estuary, appearing in these reaches within two or three months of their first appearance in the estuary. These forms left the bayous for the lake after growing to juvenile sizes. Once in Calcasieu Lake and adjacent Gulf waters, these species formed the basis of the area's commercial fisheries.

Members of category C (marine species that visit the estuary as adults) included a different set of species in every season. Winter species included *U. floridana, P. tribulus, A. probatocephalus* and *P. cromis*. Spring species included *L. brevis, U. floridana, T. lepturus*, and *P. burti*. Species characteristic of summer were *A. felis, Bagre marinus* and *P. alepidotus. Etropus crossotus* and *Syngnathus louisianae* were summer-fall species. Members of this category were readily collected by trawl, but not by seine. These forms enter the estuary as adults, and either prefer deeper water or can easily evade a seine. Members of this category that were collected by seine included small species (*S. louisianae*) or slow-moving, sedentary species (*e.g., A. felis, Gobiesox strumosus*).

Category D (anadromous and catadromous forms) included only *Alosa chrysochloris* among species collected in the Calcasieu Estuary. It was commonly found in summer and fall in the south end of Calcasieu Lake, in salinities similar to those of the Gulf of Mexico. As pointed out by Thompson and Fitzhugh (1986), migration of such species may be disrupted by the saltwater barrier at the head of the Calcasieu Estuary (which also alters the salinity and temperature regimes of the upper estuary).

Truly-estuarine species (Category E) included species of *Palaemonetes*, and members of the families Cyprinodontidae and Atherinidae. Species in this category tended to be small-sized shore-dwellers. Thus, they were well represented in seine samples, but occurred rarely in trawl samples. This group included those species most characteristic of marshy shorelines (especially certain cyprinodontids). Members of this group were also tolerant

of low salinity and could often be found in freshwater tributaries (*e.g., P. pugio, C. variegatus, F. grandis* and *Syngnathus scovelli*; Felley 1987a). Species in this category showed seasonal cycles of abundance, and some species groups showed patterns of seasonal replacement throughout the year. For example, in Calcasieu Lake, species of *Palaemonetes* showed patterns of abundance and replacement similar to those found by Subrahmanyam and Coultas (1980) in a Florida salt-marsh: *P. pugio* was the dominant species throughout the year, *P. intermedius* was most abundant in winter and spring, and *P. vulgaris* was only found in fall and winter. In seasons when they were not collected from Calcasieu Lake, *P. intermedius* and *P. vulgaris* may have moved to areas which were not sampled (perhaps into the waterways of prairie areas surrounding the lake).

Freshwater species (category F) formed an identifiable assemblage within the bayous (Felley 1987a), but were a minor component of Calcasieu Lake. They appeared in estuarine habitats primarily in winter and spring, when high rainfall and runoff produced low-salinity conditions. Felley (1987a) found that most freshwater forms retreated to the upstream areas of the bayous in summer and fall (when high-salinity water intruded into the bayous). Thus, freshwater forms showed a seasonal pattern of occurrence that was directly opposite of species in category A. Salt-tolerant freshwater forms such as *D. cepedianum* and *Dorosoma petenense* occurred irregularly in the lake throughout the year.

Classifying species by both life-history and by occurrence in particular spatio-temporal assemblages (identified by DCA) revealed the following patterns. Members of groups A and F were apparently intolerant of the range of variation of physicochemical parameters in the estuary, and appeared only when the estuary's physicochemistry approached marine or freshwater conditions, respectively. The other groups were tolerant of estuarine conditions and appeared in the estuary according to schedules dictated by their life-histories. Among these species, the truly-estuarine species (category E) appeared year-round (though some showed dramatic cycles of abundance). The more sedentary category-E forms predominated among the species characteristic of low-energy shorelines, while many members of categories B, C, and D (migratory, actively-swimming forms) predominated along high-energy shorelines. Members of categories B and C appeared in seasonal "waves". Members of category B demonstrate the importance of oligohaline nursery-areas in the Calcasieu drainage (Felley, 1987a). The species most important to local commercial fisheries are members of this category and several of these species use the entire estuary and appear in abundance in the freshwater reaches. Rogers, Targett and Van Sant (1984) and Rozas and Hackney (1983; 1984) have suggested the importance of oligohaline nursery-areas in other estuaries.

The two collection methods were biased against certain life-history groups. Seine sampling was biased against collection of category B adults and members of category C. Trawl sampling collected these forms, but was biased against collection of category B juveniles and members of category E.

Sampling bias associated with trawls was further reflected in DCA axis 2, which included some common species (*e.g. Mugil cephalus, Cynoscion nebulosus*) which could only be collected under conditions where they could not evade the trawl.

The patterns of distribution and their correspondence to species' life-histories match what has been found in other estuaries of the Gulf of Mexico (Gunter 1967; Livingston 1975; Subrahmanyam and Drake 1975; Subrahmanyam and Coultas 1980). These patterns are related to both environmental conditions in the estuary, and life-histories of the species. There has been disagreement, however, on the relative importance of life-history or environmental conditions as determiners of a species' appearance in an estuary. Subrahmanyam and Coultas (1980) felt that appearance of estuarine and marine species was not tied to physical factors, but was determined by life-history schedules. Conversely, McHugh (1967) stressed the importance of temperature and salinity in determining seasonal appearance of estuarine species. Dahlberg (1972) and Hackney, Burbanck and Hackney (l976) explained trends in assemblage differences in terms of salinity regimes in different habitats. Of the species collected from the Calcasieu Estuary, members of categories A and F seem limited by estuarine physicochemistry, while members of category E are not so limited. It is difficult to separate the relative importances of life-history parameters and physicochemical tolerances for species in categories B and C. These species have been under selection for both life-histories and physiological tolerances that allow them to exploit the estuary in certain seasons.

The commercially important species may be found throughout the estuary in particular seasons, and many of these species use oligohaline tributaries as nursery areas. The Calcasieu Estuary is highly productive of these species (NMFS 1986). Low-salinity areas of the estuary and its tributaries are important components maintaining this productivity (Herke *et al.* 1984; Felley 1987a), as they are in many estuaries (Rozas and Hackney 1983, 1984). The function of oligohaline nursery areas differs among species. The forms investigated here fell into two groups, based on their pattern of use. *Brevoortia patronus* and *M. undulatus* entered the oligohaline reaches at small sizes and left as they grew. Others entered at a range of sizes and remained for a particular season (*P. aztecus* and *L. xanthurus* in spring, *P. setiferus* in summer and fall).

The oligohaline reaches may be used by estuarine-marine species for a number of reasons. There may be unexploited food resources in these areas (as freshwater areas subsidize detritus and nutrients to estuaries, Post and de la Cruz 1977). These reaches may be free of some of the larger predators that exist in the estuary (*i.e.*, larger sciaenids). Finally, the freshwater environment may allow these species to rid themselves of parasites that cannot tolerate such low salinities (Rohde 1984). These reasons are obviously not mutually exclusive. As shown by Felley (1987a), human impacts reduce the value of freshwater-estuarine bayous as nursery areas. Human modifications of waterways distant from the estuary may result in reduced production of

commercially-important species. When assessing the effects of human impacts on estuaries, reduction in the value of such nursery areas should be considered. Freshwater tributaries of the estuary are an integral part of the estuarine ecosystem, and should be considered when studying the estuary.

ACKNOWLEDGMENTS

Susan M. Felley, Ron Ilg and Courtney Hackney criticized this manuscript, and portions of this manuscript were also criticized by James Hanifen and Karen Foote. The nekton portion of the CALECO project, reported here, was managed by Ron Ilg from October 1983 to April 1985. Patricia Riley, Charles White, James Austin, Lisa Briggs, Gwendolyn Henderson, David Shaheen and John Stacy aided in field and laboratory analyses. Pamela Langley aided in analysis of the data. This project was performed as a subgrant to McNeese State University from the Louisiana Department of Wildlife and Fisheries U.S. Department of Energy grant DE-FGO1-83EP31111.

LITERATURE CITED

BAXTER, K.N. and W.C. RENFRO. 1967. Seasonal occurrence and size-distribution of postlarval brown and white shrimp near Galveston, Texas, with notes on species information. *Fishery Bulletin*. 66:149-158.

DAHLBERG, M.D. 1972. An ecological study of Georgia coastal fishes. *Fishery Bulletin*. 70:323-352.

DeROUEN, L.R., R.W. HANN, D.M. CASSERLY, C. GIAMMONA and V.J. LASCARA. 1983. West Hackberry strategic petroleum reserve site brine disposal monitoring. 3 volumes. U.S. Department of Energy Final Report.

_____ and L.H. STEVENSON. 1987. Ecosystem analysis of the Calcasieu River/Lake Complex (CALECO). Final Report, 4 volumes. Louisiana Department of Wildlife and Fisheries, Baton Rouge.

FELLEY, J.D. 1987a. Nekton assemblages of three tributaries to the Calcasieu Estuary. *Estuaries*. 10:321-329.

_____. 1987b. Nekton of the Calcasieu River/Lake complex. Chapter 6. In L.R. DeRouen and L.H. Stevenson (eds.), Ecosystem analysis of the Calcasieu River/Lake complex. Louisiana Department of Wildlife and Fisheries Final Report.

_____ and S.M. FELLEY. 1986. Habitat partitioning of fishes in an urban, estuarine bayou. *Estuaries*. 9:208-218.

GAIDRY, W.J. III and C.J. WHITE. 1973. Investigations of commercially important penaeid shrimp in Louisiana estuaries. Louisiana Wildlife and Fisheries Commission Technical Bulletin 8.

GAUCH, H.G. Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, New York. 298 pp.

GEORGE, M.J. 1962. Preliminary observations of the recruitment of postlarvae and growth of juveniles of the brown shrimp, *Penaeus aztecus* Ives, in Barataria Bay. Louisiana Wildlife and Fisheries Commission, 9th Biennial Report, 1960-1961: 160-163.

GERAGHTY, J.J., D.M. MILLER, F. Van der LEEDEN and F.L. TROISE. 1973. *Water Atlas of the United States*. Water Information Center Publication, Port Washington, New York.

GOSSELINK, J.G., C.L. CORDES and J.W. PARSONS. 1979. An ecological characterization study of the chenier-plain coastal system of Louisiana and Texas. 3 volumes. U. S. Fish and Wildlife Service. FWS/OBS-78/9, 78/10, 78/11.

GUNTER, G. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico, pp. 621-638. In G.H. Lauff (ed.), *Estuaries*. American Association for the Advancement of Science Publication 83.

HACKNEY, C.T., W.D. BURBANCK and O.P. HACKNEY. 1976. Biological and physical dynamics of a Georgia tidal creek. *Chesapeake Science*. 17:271-280.

HERKE, W.H., B.D. ROGERS and J.A. GRIMES. 1984. Sabine fisheries study. Louisiana Cooperative Fishery Research Unit, Louisiana State University, Baton Rouge, Louisiana. 3 volumes.

HILL, M.O. 1974. Correspondence analysis: a neglected multivariate method. *Applied Statistics*. 23:340-354.

_____. 1979. DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell University, Ithaca, New York.

HOESE, H.D. and R.H. MOORE. 1977. *Fishes of the Gulf of Mexico, Texas, Louisiana and Adjacent Waters*. Texas A&M University Press, College Station, Texas. 327 pp.

JOHNSON, G.D. 1978. Development of fishes of the mid-Atlantic bight. Vol. III. Carangidae through Ephippidae. U.S. Fish and Wildlife Service FWS/OBS-78/12.

JONES, P.W., F.D. MARTIN and J.D. HARDY, JR. 1978. Development of fishes of the mid-Atlantic Bight. Vol I. Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service. FWS/OBS-78/12.

KENKEL, N.C. and L. ORLOCI. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology*. 67:919-928.

KILBY, J.D. 1955. The fishes of two Gulf coastal marsh areas of Florida. *Tulane Studies in Zoology*. 2:175-247.

KOBYLINSKI G.J. and P.F. SHERIDAN. 1979. Distribution, abundance, feeding and long-term fluctuations of spot, *Leiostomus xanthurus*, and croaker, *Micropogonias undulatus*, in Apalachicola Bay, Florida. *Contributions in Marine Science*. 22:149-161.

LASSUY, D.R. 1983. Species profiles: life histories and environmental requirements (Gulf of Mexico)—Gulf menhaden. U.S. Fish and Wildlife Service, Division of Biological Services FWS/OBS-82/11.2. U.S. Army Corps of Engineers, TR EL-82-4.

LAUFF, G.H. (ed). 1967. *Estuaries*. American Association for the Advancement of Science Publication 83.

LIVINGSTON, R.J. 1975. Impact of Kraft pulp-mill effluents on estuarine and coastal fishes in Apalachee Bay, Florida, USA. *Marine Biology*. 32:19-48.

McHUGH, J.L. 1967. Estuarine nekton. pp. 581-620. In G.H.Lauff (ed.), *Estuaries*. American Association for the Advancement of Science Publication 83.

NATIONAL MARINE FISHERIES SERVICE. 1986. Fisheries of the United States 1985. Current Fisheries Statistics 8380.

NELSON, W.R. AND D.W. AHRENHOLZ. 1986. Population and fishery characteristics of Gulf menhaden, *Brevoortia patronus*. *Fishery Bulletin*. 84:311-325.

PARKER, J.C. 1971. The biology of the spot, *Leiostomus xanthurus* Lacepede, and the Atlantic croaker, *Micropogonias undulatus* Linnaeus in two Gulf of Mexico nursery areas. Sea Grant Publication TAMU-SG-71-210, Texas A&M University, College Station, Texas.

POST, H.A. and A.A. DE LA CRUZ. 1977. Litterfall, litter decomposition and flux of organic material in a coastal plain stream. *Hydrobiologia*. 55:201-207.

RENAUD, M.L. 1986. Detecting and avoiding oxygen deficient sea water by brown shrimp, *Penaeus aztecus* (Ives) and white shrimp *Penaeus setiferus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*. 98:283-292.

ROGERS, G.S., T.E. TARGETT and S.B. VAN SANT. 1984. Fish-nursery use in Georgia salt-marsh estuaries: the influence of springtime freshwater conditions. *Transactions of the American Fisheries Society*. 113:595-606.

ROHDE, K. 1984. Ecology of marine parasites. *Helgolander Meeresuntersuchungen*. 37:5-33.

ROZAS, L.P. and C.T. HACKNEY. 1983. The importance of oligohaline wetland habitats to fisheries resources. *Wetlands*. 3:77-89.

_____ and _____. 1984. Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. *Estuaries*. 7:213-224.

SHLOSSMAN, P.A. AND M.E. CHITTENDEN. 1981. Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius*. *Fishery Bulletin*. 79:649-669.

SIMPSON, D.G. and G. GUNTER. 1956. Notes on habits, systematic characters and life histories of Texas saltwater Cyprinodontes. *Tulane Studies in Zoology.* 4:115-134.

ST. AMANT, L.S., J.G. BROOM and T.B. FORD. 1966. Studies of the brown shrimp, *Penaeus aztecus*, in Barataria Bay, Louisiana 1962-1965. *Proceedings of the Gulf and Caribbean Fishery Institute.* 18:1-17.

SUBRAHMANYAM, C.B. and C.L. COULTAS. 1980. Studies of the animal communities in two north Florida salt marshes. III. Seasonal fluctuations of fish and macroinvertebrates. *Bulletin of Marine Science.* 30:790-818.

_____ and S.H. DRAKE. 1975. Studies on the animal communities in two north Florida salt marshes. *Bulletin of Marine Science.* 25:445-465.

THOMPSON, B.A. AND G.R. FITZHUGH. 1986. A use attainability study: an evaluation of fish and macroinvertebrate assemblages of the lower Calcasieu River, Louisiana. Louisiana Department of Environmental Quality, Office of Water Research Report.

VETTER, R.D. 1982. Seasonal metabolic compensation in sympatric seatrout: adaptations to the estuary. *Transactions of the American Fisheries Society.* 111:193-198.

WARD, G.H. JR., N.E. ARMSTRONG and the MATAGORDA BAY PROJECT TEAMS. 1980. Matagorda Bay, Texas: its hydrography, ecology and fishery resources. U.S. Fish and Wildlife Service, Biological Services Program, Washington D.C. FWS/OBS-81/52.

WILLIAMS, A.B. 1955. A contribution to the life histories of commercial shrimp (Penaeidae) in North Carolina. *Bulletin of Marine Science.* 5:116-146.

Contributions in Marine Science. (1989) Vol. 31:119–136.

ASPECTS OF THE ECOLOGY OF THE CALANOID COPEPOD GENUS *PLEUROMAMMA* IN THE EASTERN GULF OF MEXICO

James L. Bennett and Thomas L. Hopkins

Department of Marine Science
University of South Florida
140 7th Avenue South
St. Petersburg, Florida 33701

ABSTRACT

The genus *Pleuromamma* is an important component of copepod assemblages from boreal through tropical latitudes. Four species are abundant in the eastern Gulf of Mexico, with their numerical ranking being *P. gracilis* > *P. piseki* > *P. abdominalis* > *P. xiphias*. All species are strong diel vertical migrators. Vertical distributions are complex, being uneven at night, which results from migrating and non-migrating components of each species. A size versus depth trend is apparent in that during the day, the larger late stage individuals center the deepest while at night the reverse occurs, with this group occurring shallowest. Adult males in general have their population centers deeper than adult females, a pattern more discernible at night than during the day. All four species are omnivorous and feed on phytoplankton, protozoans and metazoans (mostly crustaceans). The larger species show the greatest diet diversity. A feeding cycle is apparent with the adults of all species feeding primarily at night. Since most of the *Pleuromamma* populations occur in the 30-200 m zone at night, it is in this zone that their feeding activity is greatest. *Pleuromamma* is an important forage genus for micronekton and receives predation pressure both day and night from mesopelagic fishes and shrimps. The diel migrations of *Pleuromamma*, however, distribute populations across large vertical ranges over the diel period thus spreading out predation pressure in time and space and ensuring "sanctuary" for species maintenance.

INTRODUCTION

Species of the copepod genus *Pleuromamma* are conspicuous members of the oceanic zooplankton from boreal to tropical latitudes and because of their strong diel migratory behavior, are found throughout the upper 1000 m (Moore and O'Berry 1957; Roe 1972b, 1984; Hayward and McGowan 1979; Owre and Foyo 1967; Hopkins 1982). The genus plays a significant role in the oceanic food web and constitutes important, even preferential, forage for midwater micronekton (*e.g.*, Foxton and Roe 1974; Merrett and Roe 1974; Hopkins and Baird 1977, 1985a; Baird and Hopkins 1981; Heffernan and Hopkins 1981; Gorelova 1981; Clarke 1980, 1982; Kinzer 1982; Scotto di Carlo, Costanzo, Freisi, Guglielmo and Ianora 1982).

Aspects of a tropical-subtropical food web are being investigated in the eastern Gulf of Mexico and the importance of *Pleuromamma* in this ecosystem has been well documented (Hopkins and Baird 1977, 1981, 1985a; Heffernan and Hopkins 1981; Lancraft, Hopkins and Torres 1988). This paper presents information on the abundance, distribution and aspects of the trophic biology of members of this genus found in the eastern Gulf.

METHODS

Samples were taken on three consecutive midwater trawling cruises of the RV COLUMBUS ISELIN during June of 1975 and 1976 and September of 1977. The epipelagic zone (0-200 m) was sampled in 1975, the upper mesopelagic zone (200-500 m) in 1976 and the lower mesopelagic zone (500-1000 m) in 1977. Vertical distribution results, consequently, are based on composites of data from all three years and assume similarity in migration patterns from year to year. Horizontal tows were made at 22 depth horizons at various times in the diel period. Sampling was with collapsible plankton nets mounted in the mouth of a messenger-operated opening-closing Tucker trawl (Hopkins, Baird and Milliken 1973; Hopkins and Baird 1975). The plankton nets were of 165 μm mesh and constructed with a mouth width to length ratio of 1 to 5. The net mouth was square and either 44 × 44 cm or 66 × 66 cm in dimensions. Towing speed was 1.5-2.5 knots and tow duration was 45 minutes in the upper 50 m and 60-240 minutes at deeper horizons (Table 1). Sampling depth was monitored with wire angle measurements for tows shallower than 50 m, and with a depth transducer and digital deck readout system at deeper levels. A time-depth recorder provided a depth trace for each tow and volumes filtered were estimated with mechanical dial-type flowmeters. Only those samples for which the trawl successfully opened and closed and which exhibited relatively horizontal depth traces were analyzed (Table 1).

Collections were preserved in a seawater-formalin solution (~10% v/v) buffered with borax. For counts, samples were subdivided with a Motoda box (Motoda 1953) and one aliquot per sample was analyzed. Aliquots ranged from 1/64th to the entire collection depending on *Pleuromamma* abundance. Late stage and mature *Pleuromamma* were identified to species and the adults were sexed. Identification to species included copepodid stages III-VI for *P. abdominalis* and *P. xiphias* and stage VI for *P. gracilis* and *P. piseki*. Counts for stages IV and V of the latter two species were combined. Earlier copepodites were omitted from the analyses. A total of at least 100 *Pleuromamma* individuals were measured (± 0.1 mm) when sufficiently abundant in a sample. In our collections both the *edentata* and *typica* forms (see Steuer 1933) of *P. abdominalis* were found, although the *edentata* form was rare. These forms were not differentiated in the counts. Other species of *Pleuromamma* were each represented by single forms.

Formalin preserved individuals of each species were measured, rinsed with a small volume of fresh water, blotted dry and transferred to small preweighed aluminum containers for biomass estimates. Samples were then put under vacuum desiccation and dried to constant weight. Weighing was to the nearest 0.1 or 0.01 mg depending on sample size. Regressions for dry weight (DW) on metasome length (ML) for the four species were:

P. xiphias : Log DW = -2.11 + 0.56 ML (r^2 = 0.96)

P. abdominalis : Log DW = -2.69 + 0.91 ML (r^2 = 0.93)

P. gracilis and *P. piseki* : Log DW = -2.86 + 1.14 ML (r^2 = 0.71)

Potential organic loss from *Pleuromamma* from storage in our buffered formalin solutions was not accounted for.

The abundances of the various copepodite stages for each species were determined for every sample and means were calculated for all "replicate" samples from within a designated time period. The means were integrated over the depth horizons sampled to yield estimates of the number of individuals under 100 square meters of sea surface in the upper 1000 m of the water column. Vertical migration patterns were analyzed by determining the depth centers of populations during the day (Z_d) and night (Z_n, Z_m). Because not all individuals migrated, night distributions were strongly polymodal; consequently depth centers were calculated both for that segment of the population migrating into the upper 200 m (Z_m) and that remaining below 200 m

TABLE 1

Sampling information for RV COLUMBUS ISELIN cruises to 27 °N 86°W in the eastern Gulf of Mexico.

Cruise	Dates	Primary sampling zones (m)	Tow duration (hrs)	No. Tows	Mean sample volume (m3)
C-I	6/75	0-200	0.8-1.5	56	640
C-II	6/76	200-500	1.5-2.0	27	920
C-III	9/77	500-1000	2.0-4.0	18	1990

	Number of Tows	
Depth	Day	Night
0	4	5
5	1	1
10	3	3
15	2	4
30	1	3
50	5	4
75	-	3
100	3	6
150	1	3
200	2	2
250	-	1
300	2	3
350	2	2
400	3	2
450	2	1
500	2	2
550	3	2
600	2	2
700	2	1
800	2	1
900	2	3
1000	1	2
Total	45	56

(Z_n). Both day and night depth centers for adult stages were determined separately for males and females. The depth center was defined as that level below which 50 percent of the population of a particular stage, or sex, of a species resided. The daytime samples used in vertical distribution analysis were taken in the period of 0800 to 1700 h and the nighttime samples, in the period of 1900 to 0400 h.

Species biomasses were estimated by determining the mean weight of individuals for each size class (< 1.0 mm, 1.0-1.9 mm, 2.0-2.9 mm, 3.0-3.9 mm and > 4.0 mm) using the size-weight

regressions above, then multiplying this estimated weight by the number of individuals in each size class under 100 m^2 of sea surface.

Feeding studies utilized only females. Earlier studies have demonstrated that male diets were similar to those of females (Hayward 1980). Twenty females were sorted from collections made at the day (Z_d) and night (Z_m) centers of distribution, respectively, at 0800-1500 h and 2000-0300 h. Each specimen was cleared in lactic acid (Humes and Gooding 1964; Hayward 1980) and subjectively scored on the fraction of the stomach area filled with food using 500 × magnification. This fraction, expressed as a percent, is defined here as the feeding index. The stomach was defined as the widened portion of the alimentary canal, *e.g.* Dakin's (1908) midgut section, from the penultimate segment of the thorax to the initiation of the rostrum. A number of females had well developed eggs which obscured the gut, in which case the ovaries were removed by dissection to verify fullness scoring. In the case of *P. abdominalis*, two additional sets of 20 individuals were analyzed from periods covering dawn (0400-0800 h) and dusk (1700-2000 h) to describe the feeding cycle in greater detail. The feeding indices were compared using the non-parametric Mann-Whitney 'U' statistic (Sokal and Rohlf 1981), a two sample test based on measurement rankings.

For analysis of diet composition, the gut contents of 20 females with full stomachs of each species were spread on a microscope slide then mounted in the water base medium CMCP-AF (Macmillan Scientific Co., Inc.) and stained with acid fuchsin. The slides were examined under oil immersion and recognizable food items were tallied. Species diet compositions were compared using a modification of the information index (Travers 1971), the equation being,

$$D = \log_2 N - \frac{1}{N} \sum n_i \log_2 n_i$$

where D is the diversity index with a range of 0 - 3.33, N is the total incidence (= 100%) of all categories of food, and n_i is the incidence (%) of a single food category. The incidence of each food category was calculated as a percent of the total number of incidences of all food categories recorded from a species sample of guts (see Hopkins 1985; 1987). The ten food categories were diatoms, dinoflagellates, silicoflagellates, blue-green algae, foraminiferans, radiolarians, tintinnids, crustaceans, chaetognaths and golden-green debris.

RESULTS

Eastern Gulf Characteristics

Material for this study was collected during the summer months at 27°N 86°W (3200 m depth) in "Transition" or boundary waters (Jones 1973) adjacent to the eastern Gulf of Mexico Loop Current. The Loop is generated when water of Caribbean origin, the Subtropical Undercurrent, pulses into the Gulf as an anticyclonic intrusion which enters through the Yucatan Straits and exits through the straits of Florida (Leipper 1970; Nowlin 1971; Maul 1977; Molinari and Mayer 1980). The Loop is identifiable in the eastern Gulf by the depth of the 22°C isotherm between 150 and 200 meters; in "Transition" waters this isotherm is less than 100 m deep. The position of the Loop boundary in June of 1975 and 1976 in the eastern Gulf is shown in Figure 1A. We lack data for the position of the Loop in September of 1977, though XBT profiles indicate its absence from the vicinity of 27°N 86°W at the time of sampling.

As characteristic of stratified tropical-subtropical water masses, surface temperatures in summer are warm, 28-30°C, and the mixed layer shallow, extending to 30-50 m (Fig. 1B). Temperatures at the base of the steepest

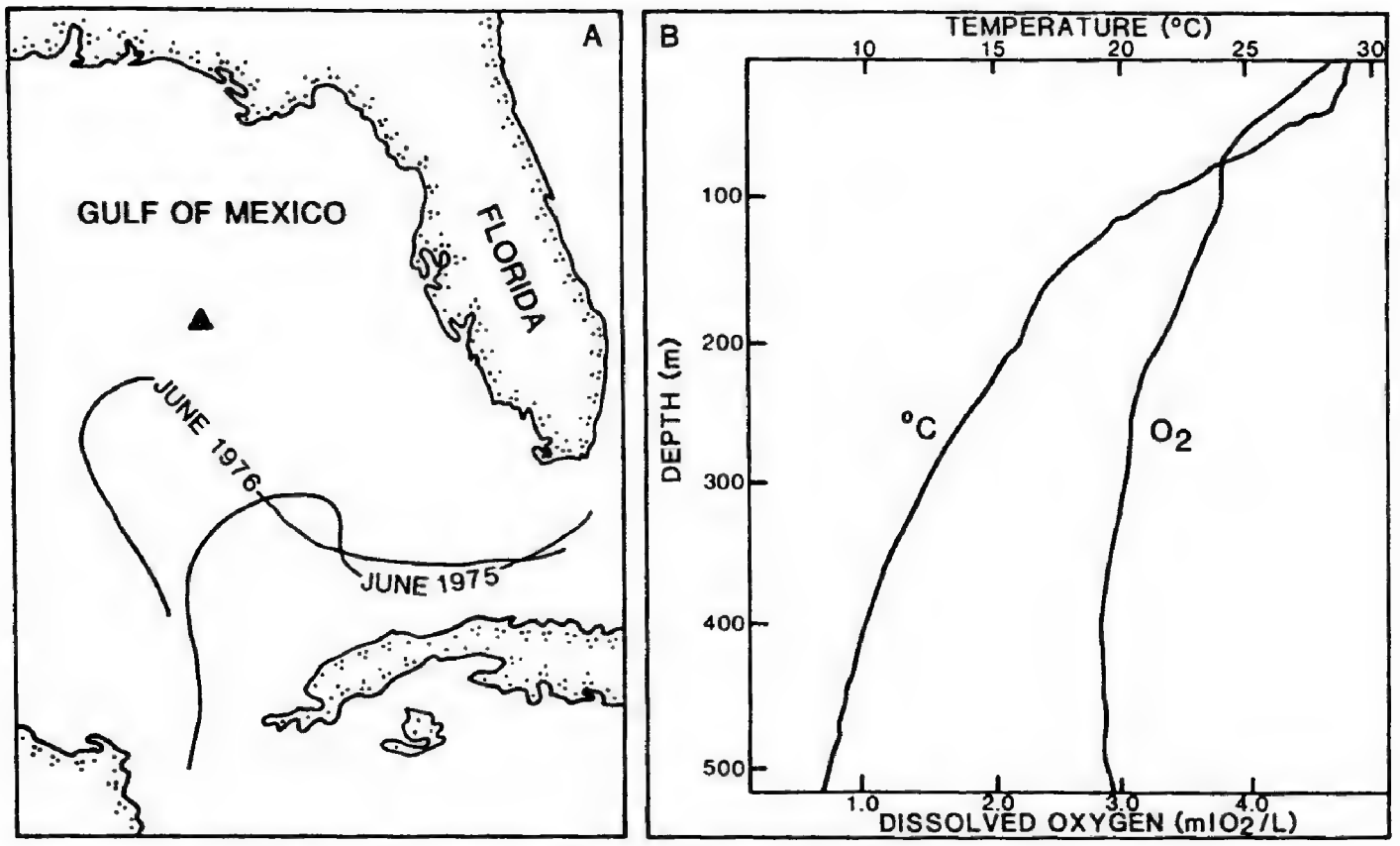


FIG. 1. (A) Sampling location (Δ) relative to the position of the Loop Current; (B) Typical summer profiles of temperature and dissolved oxygen at 27°N 86°W.

gradient of the thermocline, at approximately 150 m, are 15-18°C, then decrease to 8-9°C by 500 m, and gradually decline to 4-5°C by 1000 m. The eastern Gulf is well oxygenated, with the minimum (at ~450-500 m) exceeding 2.7 ml O_2L^{-1} (Nowlin 1971; Hopkins and Lancraft 1984). The water is oligotrophic, having an estimated productivity level of less than 50 g $C/m^2/yr$ (El-Sayed 1972; Hopkins unpublished data) and a zooplankton standing crop of 1.2 g DW/m^2 (~0.4-0.6 g $C/m^2/yr$) in the upper 1000 m (Hopkins 1982). Zooplankton species diversity is high with 21 genera individually contributing more than 1% of total zooplankton biomass in the upper 1000 m (Hopkins 1982).

Vertical Distribution; Population Structure

Pleuromamma abdominalis

The vertical distribution of this species was size related (Fig. 2). During the day adults were deepest, occurring between 300-500 m. Copepodite stages V, IV and III centered at progressively shallower depths. Adults and stage V copepodites were concentrated (> 95%) below 250m during the day whereas a large portion (33-43%) of the populations of smaller copepodites were found shallower than this depth. At night, distributions were more complex because the population had migrating and non-migrating components. Nearly all of the adults migrated into the upper 200 m at night whereas integration over sampled depth zones indicated that less than one-half

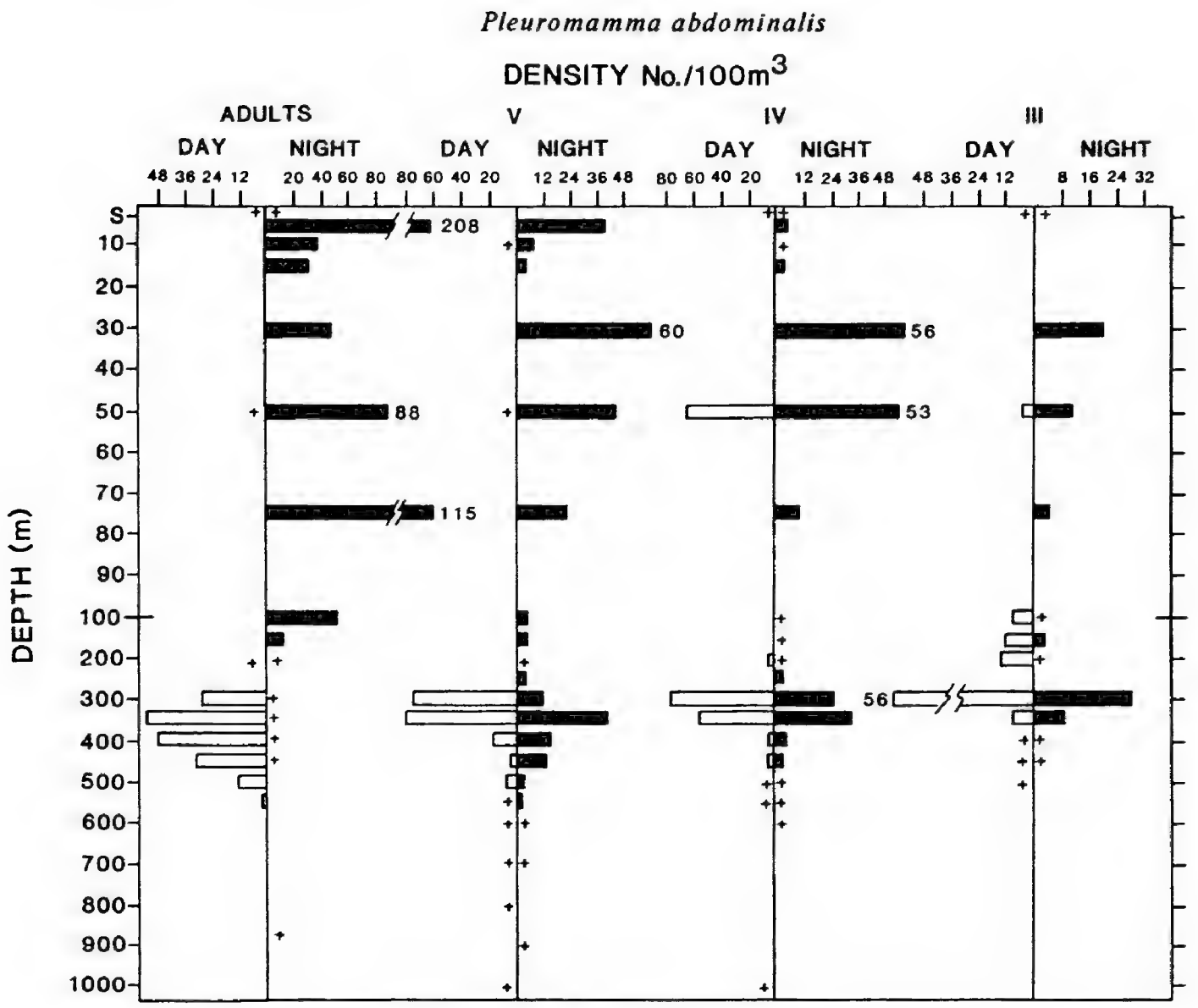


FIG. 2. Vertical distribution of *Pleuromamma abdominalis*; + indicates number ≤ 3/100 m^3.

(37%) of the pre-adult copepodites moved into this zone. Our counts showed an uneven vertical pattern for adult and copepodite V stages in the upper 200 m with maxima occurring in the 5-10 m and 50-75 m zones in the adults, and at 5-10 m and 30-50 m in stage V *P. abdominalis*. Migrating copepodite stages III and IV were mostly in the 30-50 m zone. The non-migrating components for all stages were centered below 250 m. A comparison of day-night centers of distribution for the migrating segment of the population indicated a vertical migration range of 310 m for adults and 225 m for stage III copepodites, the smallest stage considered. The female to male sex ratio for adults was approximately 2 to 1. The population center for adult males was somewhat deeper than that for females during both the day and night.

Data on standing stocks of *P. abdominalis* (Table 2) indicated that the day abundance estimate was higher than that for night (37000 *vs* 27200/100 m^2) whereas biomass values were comparable (2.8 *vs* 2.5 g DW/100 m^2). This resulted from catching proportionately more of the larger *P. abdominalis* at night. Abundances for adult through copepodite IV stages were similar while that for copepodite III was comparatively low (see Discussion). Most of the

TABLE 2

Pleuromamma populations in the upper 100 meters. Z_d = day depth center; Z_n = night depth center for non-migrating population; Z_m = night depth center for migrating population (See Methods).

Stage of Development	Total length (mm)	Numbers (No/100 m^3) Day	Numbers (No/100 m^3) Night	Biomass (mgDW/100m^2) Day	Biomass (mgDW/100m^2) Night	Sex Ratio (female:male) Day	Sex Ratio (female:male) Night	Population Depth Centers Zd	Zn	Zm
Pleuromamma xiphias										
adult		2,660	2,140	1,370	1,100	1.161	0.98:1	470	--	125
(females)	4.58	(1,430)	(1,060)					(455♀)		(125♀)
(males)	4.81							(493♂)		(143♂)
copepodite V	3.39	3,890	2,400	610	380	--	--	365	440	130
copepodite IV	2.47	4,030	1,980	270	130	--	--	300	365	95
copepodite III	1.71	3,740	1,390	130	50	--	--	250	335	55
Total		14,320	7,910	2,380	1,660					
Pleuromamma abdominalis										
adult		9,050	9,720	1,630	1,750	2.06:1	1.89:1	375	--	65
(females)	3.18	(6,090)	(6,360)					(378♀)		(56♀)
(males)	3.24	(2,960)	(3,360)					(387♂)		(89♂)
copepodite V	2.32	12,010	8,290	820	560	--	--	325	370	55
copepodite IV	1.70	10,520	6,290	290	180	--	--	300	330	44
copepodite III	1.36	5,460	2,880	90	50	--	--	275	300	50
Total		37,040	27,180	2,830	2,540					
Pleuromamma gracilis										
adult		40,630	10,350	1,520	360	2.34:1	0.81:1	300	--	80
(females)	1.81	(29,160)	(4,630)					(290♀)		(77♀)
(males)	1.76	(12,470)	(5,720)					(294♂)		(122♂)
Pleuromamma piseki										
adult		11,740	4,720	410	170	0.98:1	1.93:1	300	--	80
(females)	1.84	(5,810)	(3,110)					(311♀)		(60♀)
(males)	1.76	(5,220)	(1,610)					(305♂)		(68♂)
Pleuromamma gracilis/piseki										
copepodite V	1.39	17090	8,450	310	150	--	--	270	320	70
copepodite IV	0.82	16,280	7,160	110	50	--	--	130	250	140
Total (with adults)		85,740	30,680	2,350	730					
Grand Total		128,870	61,510	7,570	4,940					

species biomass (58-69%) was in the adults whereas numerically this stage constituted only 24-36% of the population analyzed (Table 2).

Pleuromamma gracilis, Pleuromamma piseki

Similarities in size, vertical distribution and morphology necessitated considering these two species together. Only the adults were separated to species. During the day these species showed a pattern similar to *P. abdominalis*; adults were deepest (300-400 m) while stage V copepodites centered shallower, at 200-350 m (Fig. 3). At night, as in the case of *P. abdominalis*, most of the adults migrated, with some individuals reaching

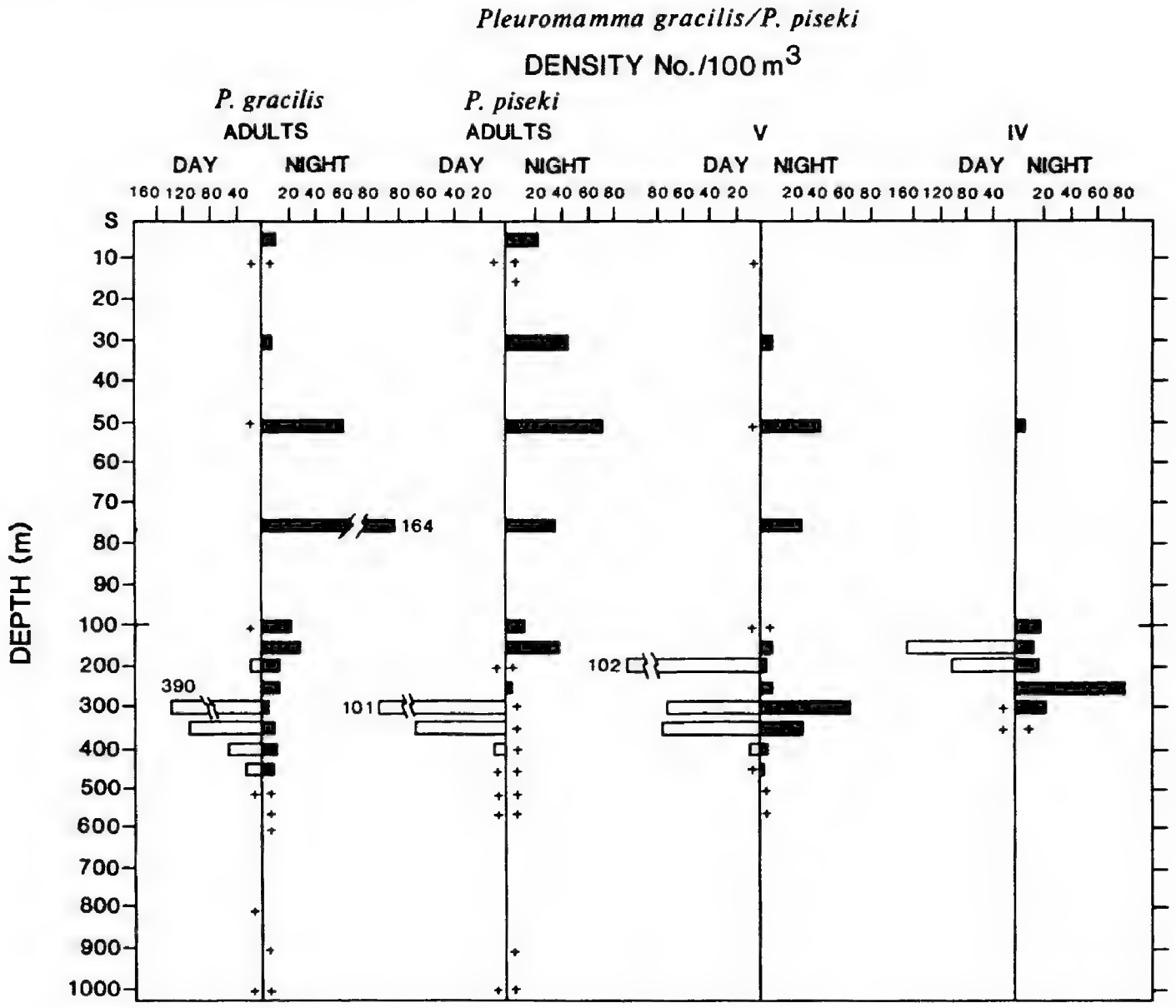


FIG. 3. Vertical distribution of *Pleuromamma gracilis* and *P. piseki*; + = ≤ 3 individuals/100 m^3. IV, V are for *P. gracilis* and *P. piseki* combined.

near-surface depths (5-10 m). The maximum for *P. piseki* was at 30-50 m and that for *P. gracilis*, somewhat deeper, at 50-75 m. Over half (56-66%) of the stage IV and V individuals remained below 200 m at night. Because of this the stage V vertical distribution was strongly bimodal, with the peak for migrators occurring at 50-75 m and for non-migrators, at 300-350 m. With the exception of a maximum at 250-300 m, stage IV had a rather even vertical distribution which extended from 100-300 m. Day-night location of population centers indicated a migration range for adult *P. gracilis* and *P. piseki* of 220-240 m, and for stages V and IV, respectively, of 200 m and < 90 m. Sex ratios for the two species were quite different in that the daytime ratios were 2.3 to 1 for *P. gracilis* and 1 to 1 for *P. piseki*. At night these reversed with the ratio for *P. gracilis* being 0.8 to 1 and for *P. piseki*, 1.9 to 1, probably a reflection of an undetermined sampling bias. Adult males and females of both species were centered at approximately the same depths during the day; at night, males were slightly deeper in the case of *P. piseki* and considerably deeper in the *P. gracilis* population.

Our integrated values for day counts were more than twice those for night (85740 *vs* 30680/100 m^2), with *P. gracilis* being much more abundant than *P. piseki* (Table 3). One half to two thirds of the net-caught biomass of these two species occurred in the adult fraction of the population.

Pleuromamma xiphias

The daytime distribution of this large species showed a clear size-related pattern in that successively older stages occurred increasingly deeper in the water column (Fig. 4). Adults, for example, were centered at 450-500 m while stage III centered at 200-350 m. Night vertical distributions were uneven, and, as with the other species, the fraction (75-85%) of the non-migrating pre-adult populations remained below 200 m. The vertical migration range for *P. xiphias* was estimated at 345 m for adults and 195-270 m for copepodite stages III-V. The adult sex ratio for *P. xiphias* was approximately 1 to 1 and centers for adult males were found to be somewhat deeper than those for females both day and night.

The daytime population estimate (128,900/m^2) was twice that for night (61,500/m^2), with most of the difference occurring in the younger stages (Table 2). As in the other species, most of the biomass (58-66%) of the net-caught *P. xiphias* occurred in the adult stage.

Feeding

The gut contents of all four species (Table 3) had common elements, though the diets of the larger species, *P. xiphias* and *P. abdominalis*, were

TABLE 3

Composition and diversity (D; See Methods) of *Pleuromamma* diets. Percentages represent incidence of occurrence, *i.e.*, the portion of the twenty individuals of each species examined having the indicated food items in their stomachs.

	Food Items (%)										
Species	Crustaceans	Diatoms	Dinoflagellates	Radiolarians	Tintinnids	Chaetognaths	Blue-green Algae	Silicoflagellates	Foraminiferans	Golden-green material	Diversity Index (D)
P. xiphias	75	50	0	40	40	0	5	5	10	100	2.54
P. abdominalis	40	60	5	50	10	5	0	15	0	100	2.41
P. gracilis	35	20	0	5	5	0	0	0	0	100	1.58
P. piseki	40	20	0	10	5	0	0	0	0	100	1.73

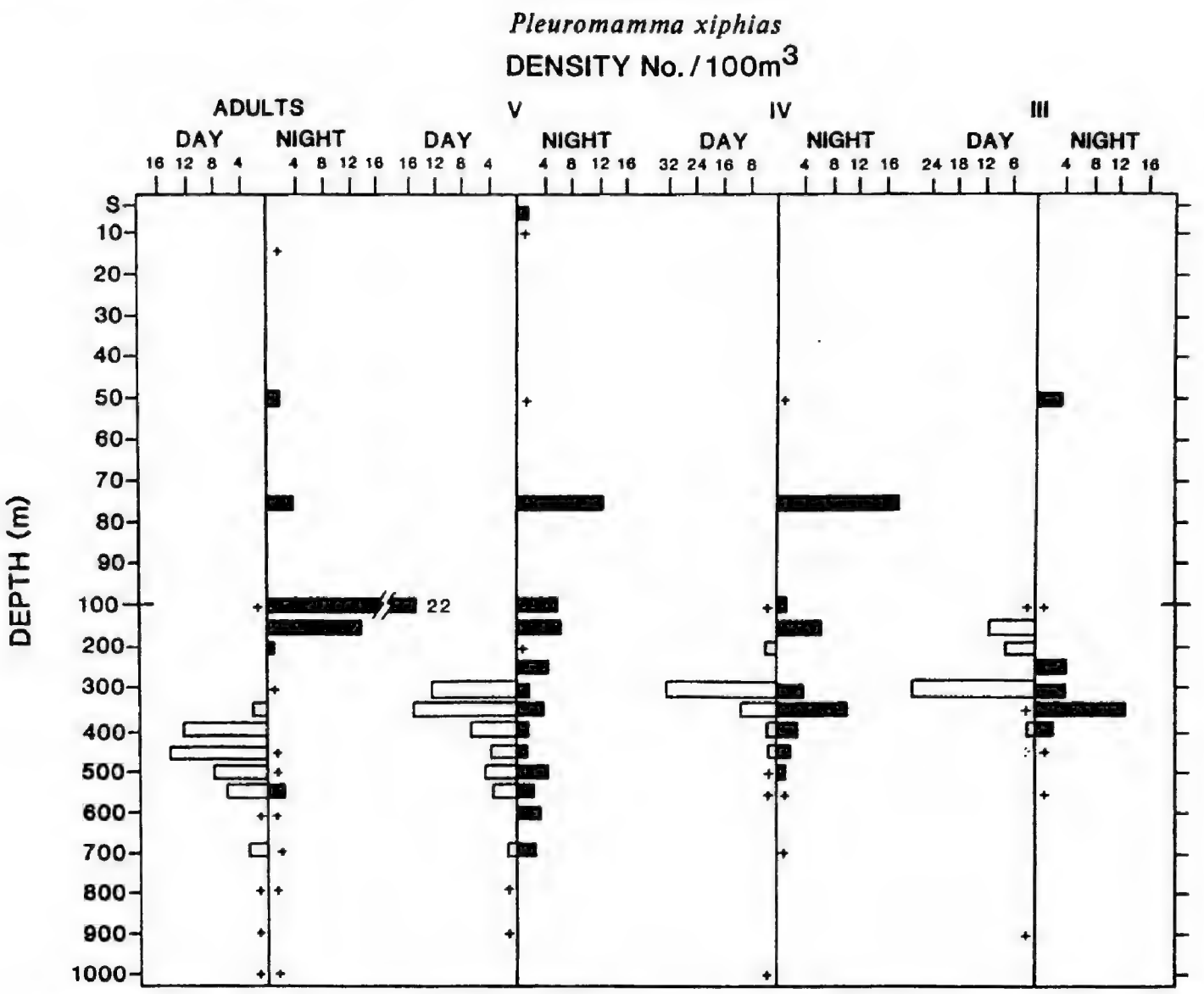


FIG. 4. Vertical distribution of *Pleuromamma xiphias*; + indicates number ≤ 3/100 m^3.

more diverse. Diet diversity indices for the two smaller species were 1.58-1.73 while those for the larger species were 2.41-2.54. The diet of all species consisted of phytoplankton (predominantly diatoms), protozoans and small crustaceans. The most ubiquitous food, found in virtually every gut, was an unidentified golden-green debris.

The Mann-Whitney 'U' test indicated that feeding was mostly at night for all members of the genus, with guts being significantly ($p < 0.05$) fuller at this time (Table 4). The more extensive data for *P. abdominalis* showed intermediate stomach fullness values for the dawn and dusk periods, these being significantly different from stomach fullness in the other diel periods at $p = 0.1$.

DISCUSSION

Population Size and Structure

The genus *Pleuromamma* is an important component of the copepod assemblage in the eastern Gulf where it contributes 10% of the copepod

TABLE 4

Average feeding index values (see Methods) for adult females (20 specimens per sample taken from their day (Z_d) and night (Z_m) centers of distribution; dawn and dusk samples taken in the upper 200 m. (–) no data.

	Time Periods			
	Dawn (0400)-0900h)	Day (0800-1500h)	Dusk (1700-2000h)	Night (2000-0300h)
Pleuromamma xiphias	-	3.35	-	51.75
Pleuromamma abdominalis	7.35	1.65	3.85	26.60
Pleuromamma gracilis	-	0.10	-	20.30
Pleuromamma piseki	-	0.01	-	23.55

biomass over the upper 1000 m (Table 3; Hopkins 1982). At night it can account for as much as 30% of the copepod biomass in the 30-200 m zone. The importance of this genus has been documented as well for other areas such as the Caribbean (Michel and Foyo 1976) the eastern North Atlantic (Roe 1972a,b) the western Sargasso Sea (Deevey and Brooks 1977) and the Bering Sea (Heinrikh 1957). The rank of abundance for adults (daytime results, Table 2) in the eastern Gulf is *P. gracilis* > *P. piseki* > *P. abdominalis* > *P. xiphias*. The same ranking is inferred from Bowman's (1971) data for the western Atlantic off Hatteras. In the eastern Atlantic off the Canary Islands, *P. piseki* is slightly more abundant than *P. gracilis* (Roe 1972b). Comparative biomass information for these species is lacking in other studies. Our data, nonetheless, indicate that in contrast to numbers, adult population biomasses are comparable for three of the species, *P. abdominalis, P. gracilis* and *P. xiphias*, with that for *P. piseki* being relatively low.

Our daytime estimates of abundance substantially exceeded those for night which is the opposite of what Roe (1972b) found for this genus and what is usually the case for zooplankton (*e.g.*, Banse 1964; Clutter and Anraku 1968; Baker 1970; Hopkins 1982). The samples discussed here were taken on midwater trawling cruises over three summers, with most of the collections from the *Pleuromamma* night zone (< 200 m) being taken on cruise C-I (1975) and those from the day zone (200-500 m) from C-II (1976). Consequently, the results potentially could be influenced by interannual variations in population size. In addition, estimates were obtained from discrete depth data rather than from continuous zone sampling, hence important population maxima or minima could have been missed (see Badcock 1970, and Longhurst and Williams 1979, for their critique of this sampling strategy).

Also, the earlier copepodite stages of all four *Pleuromamma* species were poorly sampled with our particular nets and were either missing from our collections or gave low counts. Their relative scarcity undoubtedly was the result of escapement (and extrusion; see Vannucci 1968) considering that metasome widths of the very early copepodite stages of all four species approximate or are less than the net mesh diagonal, 0.23 mm.

Vertical Distribution

Segments of the population of all four *Pleuromamma* species undergo extensive diel vertical migration which can cover hundreds of meters and traverse the thermocline. The larger species and the older stages of each species have population centers deeper in the water column during the day and migrate over longer distances. Adults of *Pleuromamma abdominalis*, for example, vertically migrate over 300 meters with those reaching the surface mixed layer being exposed to a temperature range of 18°C (see Fig. 1B). During the day *P. xiphias* is found deepest followed in ascending depth order by *P. abdominalis*, then the co-occurring *P. gracilis* and *P. piseki*. The day population depths are approximately the same as those reported by Moore and O'Berry (1957) in the Florida Current, yet with *P. xiphias* and *P. abdominalis* being shallower than indicated by Roe (1972b) in the eastern North Atlantic. Also, Roe (1972b) reported a clear separation of adults of *P. gracilis* and *P. piseki* during the day which was not evident in the present study.

An ontogenetic migration for *P. abdominalis* and *P. gracilis* has been described in the Adriatic by Shmeleva and Zaika (1973) wherein the younger stages are at depth and occupy increasingly shallow waters as they develop. At night the copepodite stage *vs* depth pattern in the eastern Gulf agrees in general with that observed in the Adriatic. During the day, however, when the genus is found mostly below 200 m, larger individuals occur deeper. This same daytime pattern has been reported as well for *P. robusta* in the North Atlantic (Longhurst and Williams 1979). It is postulated that superior swimming capabilities and faster sinking rates of the larger older stages during the twilight periods of vertical migration may be an important factor in generating the observed distributions.

As Roe (1972b) found for *P. piseki* in the northeastern Atlantic, adult males of all four species at night were centered somewhat deeper than females; thus female to male ratios at specific horizons can vary significantly over the zone of occurrence. For example, we found adult female to male ratios of 4.9 to 1 for *P. abdominalis* and 2.3 to 1 for *P. piseki* in the shallow night maxima at 5-10 m, these being much higher than mean values for their entire night zones. Also, in waters off New Zealand, Bradford (1970) observed differences in timing of upward migrations of *P. gracilis* in that males lagged behind females. Overall adult female to male ratios for *P. abdominalis* and *P. xiphias*, respectively, approximated 2 to 1 and 1 to 1 both day and night, which is probably a good estimate of their relative abundances in the eastern Gulf. The two smaller species, however, gave different ratios over the diel period. The ratio for *P. gracilis* was 2.3 to 1 during the day and 0.8 to 1 at night whereas *P. piseki* showed the reverse pattern with day and night ratios, respectively, being 1 to 1 and 1.9 to 1. Bowman (1971), also noted differences in the sex ratios of these two species. Large diel variations in sex ratios have been reported for northeast Atlantic populations of *Pleuromamma* by Roe (1972a,b) who discussed them in relation to vertical plankton layering and potential sampling

bias resulting from horizontal tows. A similar towing strategy was used in the present study and this, in combination with vertical layering in the plankton, possible time lags between migrations of males and females and possible interannual variation in sex ratios (data combined from three different years), probably accounts for much of the diel variation recorded here.

Trophic Role

The principal diet components indicate, as others have determined for this genus (*e.g.*, Heinrikh 1958; Harding 1974; Hayward 1980; Hopkins 1985), that eastern Gulf species of *Pleuromamma* are generalist omnivores. Phytoplankton, protozoans and metazoans (mostly crustaceans) were common to the diets of all four species, with the diets of the larger species being more diverse. This is in keeping with data from Antarctic copepod assemblages that show, in general, diet diversity of herbivores and omnivores increases with species size (Hopkins 1985). Our data indicate that (as Hayward (1980) found for this genus in waters off California) most foraging, at least in adults, occurs at night. Much of the population, especially juvenile stages, remains at depth (> 200 m) at night, however, and their feeding periodicity was not investigated. Our recent findings for *Euchaeta marina* in the eastern Gulf indicate that the juveniles of this species, at least, show far less diel periodicity in feeding than the adults (Shuert and Hopkins 1987). While the diel feeding pattern for *Pleuromamma* is characteristic of many species of migrating zooplankton and micronekton (*e.g.*, Hayward 1980; review in Hopkins and Baird 1977) the standard caveats apply here as they do for all studies of migrating zooplankton based on net collections. For example, daytime tows were deeper, thus allowing for longer gut clearance time. Also, the shallower nighttime tows potentially collected more phytoplankton and thus had more available for net feeding. The contribution of these factors to observed trends is unknown.

Pleuromamma, because of its abundance and co-occurrence with much of the predatory micronekton both day and night, is an important forage genus in the eastern Gulf and elsewhere (Merrett and Roe 1974; Gorelova 1978, 1981; Clarke 1980; Hopkins and Baird 1981, 1985a,b; Hopkins 1982). Members of this genus, the larger species in particular, are often preferred food (*e.g.*, Merrett and Roe 1974; Clarke 1980; Baird and Hopkins 1981; Hopkins and Baird 1985a; Lancraft *et al.* 1988). Mesopelagic fishes and shrimps concentrate in the upper 200 m zone at night (*e.g.*, Hopkins 1982; Flock and Hopkins 1987) where the migrating component of *Pleuromamma* populations are most abundant. Our diet analyses show, for example, that two abundant midwater fishes, *Lampanyctus alatus* and *Gonostoma elongatum*, feed selectively on *Pleuromamma*, this genus comprising a large fraction of their daily ration (Hopkins and Baird 1985; Lancraft *et al.* 1988). Their respective removal rates are estimated at 0.14-0.34% and 0.26% of the > 1 mm *Pleuromamma* numbers which comprises only a small portion of the total population. As evident from Figure 5, however, a large number of

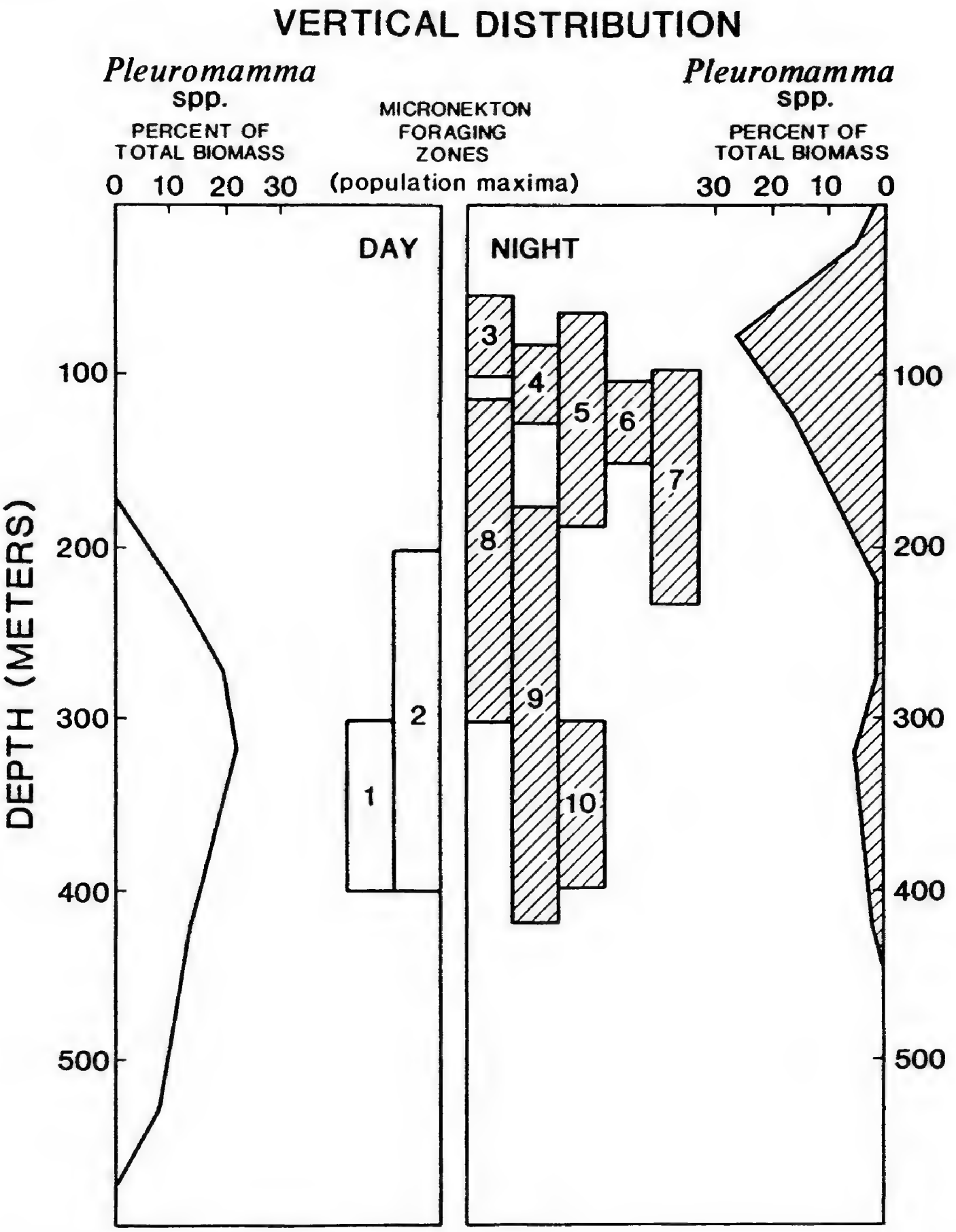


FIG. 5. Diel vertical distribution of *Pleuromamma* (biomass of >1.5 mm population) in relation to that of micronekton predators known to feed on this genus in the eastern Gulf of Mexico. Rectangles include only the vertical range of the population maximum, and not the entire depth range of the species in each group. This figure modified from Fig. 6 in Bennett (1986).

DAY FORAGERS

Group 1. Sternoptychid fish: *Valenciennellus tripunctulatus* [1]
Group 2. Sternoptychid fish: *Argyopelecus hemigymnus* [1]

NIGHT FORAGERS

Group 3. Squid: *Pterygioteuthus gemmata* [5]
Myctophid fishes: *Benthosema suborbitale, Diaphus mollis, D. perspicillatus, D. taaningi, Hygophum macrochir* [1]
Group 4. Myctophid fishes: *Diaphus dumerilii, Hygophum taaningi, Lampanyctus alatus, Lepidophanes guentheri, Notoscopelus resplendens* [1]
Group 5. Squid: *Pyroteuthis magaritifera* [5]
Myctophid fish: *Diaphus problematicus* [1]
Penaeid shrimps: *Sergestes corniculum* (group), *Sergestes pectinatus, Sergia splendens* [3]
Group 6. Myctophid fishes: *Diaphus rafinesquii, Lampanyctus nobilis* [1]
Penaeid shrimp: *Gennadas scutatus* [2]
Group 7. Squid: *Pterygioteuthis giardi* [5]
Penaeid shrimp: *Sergestes sargassi* [3]
Caridean shrimp: *Systellaspis debilis* [4]
Group 8. Myctophid fish: *Lampanyctus lineatus* [1]
Penaeid shrimp: *Sergia robustus* [3]
Group 9. Penaeid shrimp: *Gennadas valens* [2]
Group 10. Cardean shrimp: *Acanthephyra purpurea* [4]

---

[1] Gartner, Hopkins, Baird and Milliken 1987; Hopkins and Baird 1977; Hopkins unpublished data
[2] Heffernan and Hopkins 1981
[3] Flock and Hopkins unpublished data
[4] Lancraft, *et al.* 188; Flock and Hopkins unpublished data
[5] Passarella unpublished data

micronekton species prey on this genus throughout the diel period and the cumulated effect of all micronekton species utilizing this resource must be determined before the impact of micronekton on this genus can be assessed. In any case, the large vertical migrations spread out predation in time and space to such a degree that a sufficient fraction of the *Pleuromamma* breeding population has "sanctuary" thus ensuring the maintenance of these species.

LITERATURE CITED

BADCOCK, J. 1970. The vertical distribution of mesopelagic fishes collected on the SOND cruise. *Journal of the Marine Biological Association, U.K.* 50:1001-1044.

BAIRD, R.C., and T.L. HOPKINS. 1981. Trophodynamics of the fish *Valenciennellus tripunctulatus*, II. Selectivity, grazing rates and resource utilization. *Marine Ecology - Progress Series.* 5:11-19.

BAKER, A. de C. 1970. The vertical distribution of euphausiids near Fuerteventura, Canary Islands. *Journal of the Marine Biological Association, U.K.* 50:301-342.

BANSE, K. 1964. On the vertical distribution of zooplankton in the sea. *Progress in Oceanography.* 2:53-125.

BENNETT, J.L. 1986. Vertical distribution, abundance and feeding of the copepod genus *Pleuromamma* in the eastern Gulf of Mexico. Masters Thesis. University of South Florida. 50 pp.

BOWMAN, T.S. 1971. The distribution of calanoid copepods off the south-eastern United States between Cape Hatteras and southern Florida. *Smithsonian Contributions to Zoology.* 96. 58 pp.

BRADFORD. J.M. 1970. Diurnal variation in vertical distribution of pelagic copepods of Kaikoura, New Zealand. *New Zealand Journal of Marine and Freshwater Research.* 4:337-350.

CLARKE, T.A. 1980. Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters. *Fishery Bulletin, U.S.* 74:619-640.

_____. 1982. Feeding habits of stomiatoid fishes from Hawaiian Waters. *Fishery Bulletin, U.S.* 80:287-304.

CLUTTER, R.I. and M. ANRAKU. 1968. Avoidance of samplers. Pages 57-76 in D.J. Tranter, ed. *Monographs for oceanographic methodology.* 2. Zooplankton sampling. The UNESCO Press, Paris.

DAKIN, W.J. 1908. Notes on the alimentary canal and food of the copepod. *Internationale Revue der Gesamten Hydrobiologie.* 1:772-782.

DEEVEY, G.B. and A.L. BROOKS. 1977. Copepods of the Sargasso Sea off Bermuda: species composition and vertical and seasonal distribution between the surface and 2000 meters. *Bulletin of Marine Science.* 27:256-291.

EL-SAYED, S.Z. 1972. Primary productivity and standing crop of phytoplankton. pp. 8-13. In V.C. Bushnell, (ed.) *Chemistry, Primary Productivity, and Benthic Algae of the Gulf of Mexico.* Serial Atlas of the Marine Environment, American Geophysical Society Folio 22.

FLOCK, M.E. and T.L. HOPKINS. 1987. The vertical distribution and feeding ecology of sergestid shrimps in the eastern Gulf of Mexico. Abstract 31G-01. *EOS* 68:1731.

FOXTON, P. and H.S.J. ROE. 1974. Observations on the nocturnal feeding of some mesopelagic decapod crustaceans. *Marine Biology.* 28:37-49.

GARTNER, J.V. JR., T.L. HOPKINS. R.C. BAIRD aod D.M. MILLIKEN. 1987. The lanternfishes (Pisces: Myctophidae) of the eastern Gulf of Mexico. *Fishery Bulletin, U.S.* 85:81-98.

GORELOVA, T.A. 1978. The feeding of lanternfishes *Ceratoscopelus warmingii* and *Bolinichthys longipes*, of the family myctophidae in the western equatorial part of the Pacific Ocean. *Journal of Ichthyology.* 13:673-683.

_____. 1981. Notes of feeding and gonad condition in three species of the genus Gonostoma (Gonostomatidae). *Journal of Ichthyology.* 25:82-92.

HARDING. G.C.H. 1974. The food of deep-sea copepods. *Journal of the Marine Biological Association, U.K.* 54:141-155.

HAYWARD, T.L. 1980. Spatial and temporal patterns of feeding of oceanic copepods from the north Pacific central gyre. *Marine Biology.* 58:295-309.

_____ and J.A. McGOWAN. 1979. Pattern and structure in an oceanic zooplankton community. *American Zoologist.* 19:1045-1055.

HEFFERNAN, J.J. and T.L. HOPKINS. 1981. Vertical distribution and feeding of the shrimp genera *Gennadas* and *Bentheogennema* (Decapoda: Penaeidea) in the eastern Gulf of Mexico. *Journal of Crustacean Biology.* 1:461-472.

HEINRIKH, A.K. 1957. Vertical plankton distribution in the area of southeast of Boninskii Island. *Doklady Akademii nauk SSSR.* 117:1007-1010.

_____. 1958. On the nutrition of marine copepods in the tropical region. *Doklady Akademii nauk SSSR.* 119:1028-1031.

HOPKINS, T.L. 1982. The vertical distribution of zooplankton in the eastern Gulf of Mexico. *Deep-Sea Research.* 29:1069-1083.

_____. 1985. Food web of an Antarctic midwater ecosystem. *Marine Biology.* 89:197-212.

_____ 1987. Midwater food web in McMurdo Sound., Ross Sea, Antarctica. *Marine Biology.* 96:93-106.

_____ and R.C. BAIRD. 1975. Net feeding in mesopelagic fishes. *Fishery Bulletin, U.S.* 73:903-914.

_____ and _____. 1977. Aspects of the feeding ecology of oceanic midwater fishes. pp. 325-360. In N.R. Anderson and B.J. Zahuranec, (eds.) *Proceedings of an International Symposium on Prediction of Sound Scattering in the Ocean.* Plenum Press, New York.

_____ and _____. 1981. Trophodynamics of the fish *Valenciennellus tripunctulatus.* I. Vertical distribution, diet and feeding chronology. *Marine Ecology - Progress Series.* 4:1-10.

_____ and _____. 1985a. Aspects of the trophic ecology of the mesopelagic fish *Lampanyctus alatus* (Family Myctophidae) in the eastern Gulf of Mexico. *Biological Oceanography*. 3:285-313.

_____ and _____. 1985b. Feeding ecology of four hatchet fishes (Sternoptychidae) in the eastern Gulf of Mexico. *Bulletin of Marine Science*. 36:260-277.

_____, _____ and D.M. MILLIKEN. 1973. A messenger-operated closing trawl. *Limnology and Oceanography*. 18:488-490.

_____ and T.M. LANCRAFT. 1984. The composition and standing stock of mesopelagic micronekton at 27°N 86°W in the eastern Gulf of Mexico. *Contributions in Marine Science*. 27:143-158.

HUMES, A.G. and R.U. GOODING. 1964. A method for studying the external anatomy of copepods. *Crustaceana* 6:238-240.

JONES, J.I. 1973. Physical oceanography of the northeast Gulf of Mexico and Florida Continental Shelf area. Sec. IIB. pp. 1-11. In State University System of Florida Institute of Oceanography (Coordinator), James I. Jones *et al.* (eds) *A Summary of Knowledge of the Eastern Gulf of Mexico.*

KINZER, J. 1982. The food of four myctophid fish species off northwest Africa. *Rapport et Proces-verbaux Reunion Conseil Internationale Exploration de la Mer*. 180:385-390.

LANCRAFT. T.M., T.L. HOPKINS and J.J. TORRES. 1988. Aspects of the ecology of the mesopelagic fish *Gonostoma elongatum* (Gonostomatidae, Stomiiformes) in the eastern Gulf of Mexico. *Marine Ecology - Progress Series*. 49:27-40.

LEIPPER, D.F. 1970. A sequence of current patterns in the Gulf of Mexico. *Journal of Geophysical Research*. 75:637-657.

LONGHURST, A. and R. WILLIAMS. 1979. Materials for plankton modeling: vertical distribution of Atlantic zooplankton in summer. *Journal of Plankton Research*. 1:1-28.

MAUL, G.A. 1977. The cycle of the Gulf Loop Current. Part I. Observations during a one year time series. *Journal of Marine Research*. 35:29-47.

MERRETT, N.R. and H.S.J. ROE. 1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. *Marine Biology*. 28:115-126.

MICHEL, H.B. and M. FOYO. 1976. Caribbean zooplankton, Part 1. Siphonophora, Heteropoda, Copepode, Eupharisiacea, Chaetognatha and Salpidae. Report to the Office of Naval Research, 549 pp.

MOLINARI, R.L. and D. MAYER. 1980. Physical oceanographic conditions at potential OTEC site in the Gulf of Mexico; 27°N; 85.5°W. NOAA Technical Memorandum ERL AOML. No. 42. 99pp.

MOORE, H.B. and D.L. O'BERRY. 1957. Plankton of the Florida Current IV. Factors influencing the vertical distribution of some common copepods. *Bulletin of Marine Science of the Gulf and Caribbean*. 7:297-315.

MOTODA, S. 1953. New plankton samplers. *Bulletin of the Faculty of Fisheries, Hokkaido University*. 3:181-186.

NOWLIN, W.D. 1971. Water masses and general circulation of the Gulf of Mexico. *Oceanography International*. 6:28-33.

OWRE, H.B. and M. FOYO. 1967. Copepods of the Florida Current. *Fauna Caribaea*. 1. 137 pp.

ROE, H.S.J. 1972a. The vertical distribution and diurnal migrations of calanoid copepods collected on the SOND Cruise, 1965. I. The total population and general discussion. *Journal of the Marine Biological Association, U.K.* 52:277-314.

_____. 1972b. The vertical distribution and diurnal migrations of calanoid copepods collected on the SOND cruise. 1965. III. Systematic account: families Euchaetidae up to and including the Metridiidae. *Journal of the Marine Biological Association, U.K.* 52:525-552.

_____. 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 4. The copepods. *Progress in Oceanography*. 13:353-388.

SCOTTO di CARLO, B., G. COSTANZO. E. FRESI, L. GUGLIELMO and A. IANORA. 1982. Feeding ecology and stranding mechanisms in two lanternfishes, *Hygophum benoiti* and *Myctophum punctatum. Marine Ecology - Progress Series*. 9:13-24.

SHMELEVA, A.A. and V.Y. ZAIKA. 1973. Vertical distribution of copepodid stages of copepods in the adriatic sea. *Oceanology*. 13:722-725.

SHUERT, P.G. and T.L. HOPKINS. 1987. The vertical distribution and feeding ecology of *Euchaeta marina* in the eastern Gulf of Mexico. *Contributions in Marine Science*. 30:49-61.

SOKAL, R.R. and F.J. ROHLF. 1981. *Biometry*. W.H. Freemen and Company, New York. 859 pp.

STEUER, A. 1933. Bericht über die Bearbeitung der Copepodengattung *Pleuromamma* Giesbr. 1898 der Deutschen Tiefsee-Expedition "Valdivia". *Thalassia*. 1:1-48.

TRAVERS, M. 1971. Diversité di microplancton du Golfe de Marseille en 1964. *Marine Biology*. 8:308-343.

VANNUCCI, M. 1968. Loss of organisms through the meshes. pp. 77-86. In D.J. Tranter, (ed.) *Monographs on Oceanographic Methodology*. 2. Zooplankton Sampling. The UNESCO Press, Paris.

Contributions in Marine Science. (1989) Vol. 31:137–146.

MORTALITY OF LARVAL RED DRUM *(SCIAENOPS OCELLATUS)* ASSOCIATED WITH A *PTYCHODISCUS BREVIS* RED TIDE

Cecilia M. Riley, Scott A. Holt, G. Joan Holt, Edward J. Buskey and C.R. Arnold

University of Texas at Austin
Marine Science Institute
Port Aransas, Texas 78373-1267

ABSTRACT

Historically, the occurrence of red tides in Texas coastal waters has not been well documented. The most recent bloom of the red tide organism *Ptychodiscus brevis* occurred during October and November, 1986, a time of year when many species of commercially important fish spawn and their larvae are abundant in local estuaries. Peak density of *P. brevis* averaged 7,000 cells/ml at monitoring sites but transient patches of extremely high concentrations (10,000-47,680 cells/ml) were commonly found in the bays near Port Aransas during the entire month of October. Hatch rates of laboratory spawned red drum eggs were unaffected by all red tide concentrations tested. However, once hatched, larvae were negatively affected by all concentrations > 40 cells/ml, based on dilution experiments with natural populations of *P. brevis*. Larval fish displayed abnormal swimming behavior followed by paralysis prior to death. Similar results were obtained during field tests with wild caught juvenile red drum. Red tides occurring during spawning periods could result in reduced recruitment of the affected year-class in following years.

INTRODUCTION

About twenty species of dinoflagellates known to cause red tides contain toxins that can cause respiratory irritation in humans, contaminate shellfish or kill fish (Steidinger 1983). In Texas coastal waters, red tides can be caused by the dinoflagellates *Ptychodiscus brevis* (formerly called *Gymnodinium breve*) or *Gonyaulax monilata*. Although the historical occurrence of red tides along the Texas coast is poorly documented, it is believed that there have been three *P. brevis* red tides and six or seven *G. monilata* red tides since the earliest documented red tide in 1935 (Wilson and Ray 1956; Snider 1986). Red tides with fish kills probably associated with *P. brevis* were reported as early as 1844 off the west coast of Florida (Steidinger and Joyce 1973). The causal organism was identified in 1947 by Dr. C. C. Davis (Steidinger and Joyce 1973). Florida red tides caused by *P. brevis* occur nearly every year and have been well documented in the past three decades.

P. brevis red tides are believed to originate in offshore waters (> 16 km) in depths of 12 to 37 m in Florida (Steidinger 1975). It is assumed that *P. brevis*, like some other dinoflagellates, form benthic resting cysts which help explain their seasonal abundance patterns. Typical background levels for this organism are < 1000 cells/liter for both inshore and offshore Gulf waters, so concentrations significantly above this level may suggest the formation of a bloom. However, the factors that influence bloom formation have not been positively identified. Some of the proposed mechanisms include upwelling and intrusion of loop currents (Haddad and Carder 1979; Seliger, Tyler and McKinley 1979) and seasonal changes in nutrient concentrations (Dugdale 1979). The suppression of zooplankton grazing rates has also been postulated as having a role in the initiation of dinoflagellate blooms (Huntley 1982; Huntley, Sykes, Rohan and Marin 1986). Temperature and salinity may also have a pronounced effect on both the initiation and maintenance of *P. brevis* blooms. Laboratory studies indicate that the optimal temperature and salinity ranges for *P. brevis* are 16-27°C and 27-37‰ S respectively (Rounsefell and Nelson 1966; Steidinger and Ingle 1972). These environmental conditions, required for *P. brevis* blooms, correspond to a time of year when many species of larval fish inhabit south Texas estuaries. Although many studies have documented the toxic effects of red tide organisms on various species of shellfish (Sievers 1969; Wardle, Ray and Aldrich 1975; Roberts, Henderson and Medlyn 1979) and adult fish (Sievers 1969; Steidinger and Ingle 1972) there have been no published report of studies involving *P. brevis* toxicity on larval fish, many of which are commercially valuable to the fishing industry. Red tides occurring during spawning periods could decrease the survival of larval fish and possibly result in a significant reduction in year-class strength for the affected cohort.

Our objectives were to 1) monitor the population density of *P. brevis* and 2) determine the effects of *P. brevis* toxins on hatch rates and survival of larval red drum (*Sciaenops ocellatus*). We also designed an experiment to control for effects that may occur when fish were exposed to cells of *P. brevis* in small, closed containers (*i.e.*, laboratory conditions) as opposed to what might occur in a natural situation where *P. brevis* occurs in patches surrounded by unaffected water.

Finally, we report effects of the 1986 red tide on population density of larval red drum from Aransas Pass and Lydia Ann Channel sites in the western Gulf of Mexico that are monitored on a regular basis.

METHODS

The population density of *P. brevis* was monitored daily from 28 September to 5 November 1986 with water samples collected from two sites in Port Aransas (Fig. 1). Site 1 was the University of Texas at Austin Marine Science Institute (UTMSI) pier located approximately one mile from the mouth of the Port Aransas jetties. Site 2 was the pier at UTMSI Fisheries and Mariculture Center located in the Corpus Christi Ship Channel, approximately 3 miles inshore of the jetty mouth. Water samples from each site were collected from the surface in 5 liter buckets. The sample was mixed and a 250 ml aliquot was drawn from it and preserved and stained with Lugol's Iodine. Cell

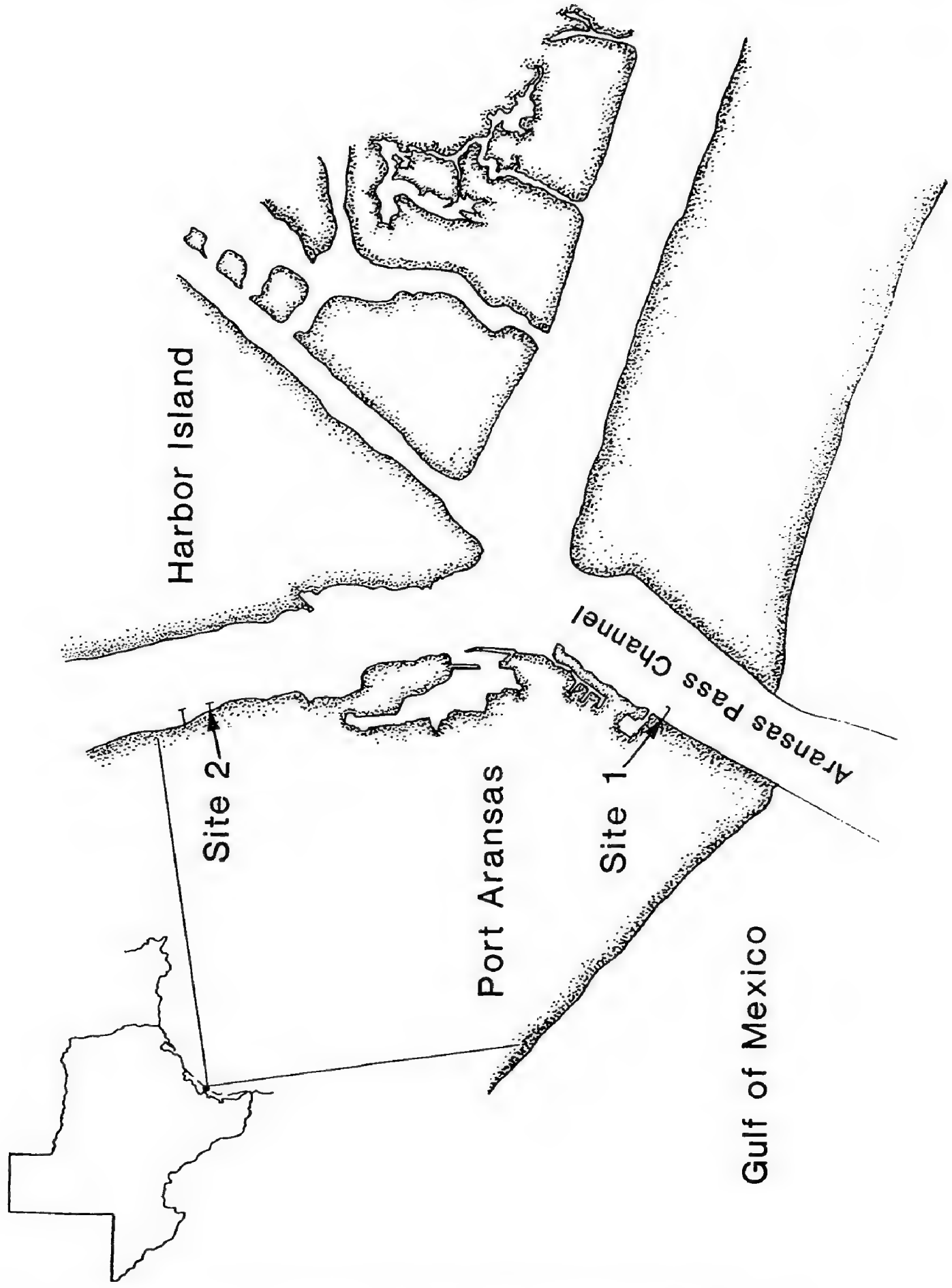


FIG. 1. Water collection sites for determination of *P. brevis* concentration.

density of each sample was determined by averaging counts from 3 replicate 0.1 ml subsamples of the aliquot and recorded as mean cells/ml.

Research has shown that in some laboratory cultures of *P. brevis* cells counts were correlated with toxicity measured as "mouse units" but that was not true for all cultures (Spikes, Ray, Aldrich

and Nash 1968). In this study toxin levels were not measured directly through mouse bioassays; instead, larval fish were exposed to toxins released from both whole and dead cells, a situation more likely to be experienced by wild larval fish during a red tide outbreak.

Density estimates for larval red drum were made using standard ichthyoplankton sampling techniques in the Aransas Pass Channel near the UTMSI pier. Samples were taken weekly from 23 September to 28 October 1986 with a 0.5 m diameter conical net with 505 μm mesh towed at the surface for approximately three minutes. The net was equipped with a flowmeter to measure water volume sampled. Samples were taken in duplicate or triplicate and the catch was expressed as mean number/100m^3.

Laboratory spawned red drum (for details on spawning techniques see Arnold, Bailey, Williams, Johnson and Lasswell 1977) eggs were used to determine the toxic effects of *P. brevis* on hatch rates. A small number of eggs (~20-40) were counted and placed into 100 ml pyrex beakers which contained either filtered sea water (control) or sea water containing various concentrations of *P. brevis*. In three experiments, eleven different concentrations of *P. brevis* were obtained by making dilutions of naturally occurring very high concentrations collected in the field. Actual cell concentrations in each dilution were determined by counting three replicate 0.1 ml subsamples both before and after the experiments. Variability among subsample counts was relatively low. One standard error of the mean averaged 10.6% of the mean and ranged from 4 to 22% for all determinations of both experimental and field concentrations. Three replicates of each treatment (controls and various concentrations of *P. brevis*) were set up in a completely randomized design (Hurlbert 1984) and fish eggs were allowed to hatch. The following day the number of dead eggs and number of larvae were counted to determine hatch rate and beakers still containing live larvae were maintained to determine the mortality rate after 24 h of exposure to the various concentrations of *P. brevis*. This experimental procedure was repeated 3 times throughout the study period using different concentrations of *P. brevis* and controls.

We tested for the presence of toxic effects on older red drum larvae (21 days old) in a similar manner. One liter beakers were filled with filtered sea water (control) or sea water containing *P. brevis* concentrations of 2040, 420 and 30 cells/ml. Fish were placed in each beaker and timed until death.

Because of the fragile nature of *P. brevis* cells (as evidenced by the fact that they are easily broken-up by the surf, releasing toxins into the sea spray) we suspected that laboratory handling of the red tide organism could increase their toxicity beyond that of a natural bloom. We designed an experiment to ascertain differences in *P. brevis* toxicity in laboratory versus field conditions using one month old red drum. The bottoms and large side segments of four 4 liter plastic pails were removed and replaced with fine mesh (2mm) so that fish were unable to escape but water and *P. brevis* cells could move in and out freely. Styrofoam blocks were glued to the rims of the pails for flotation. A boat was anchored in an area of Redfish Bay which had a high concentration of *P. brevis* (assumed due to the reddish color of the water and later determined to be 47,680 cells/ml). Two experimental pails were floated directly in the bay at a depth of ~12 cm (simulating natural exposure to toxins) and two were placed into separate containers filled with the same water, dipped-up from the surface layer to a depth of ~20 cm and poured into the buckets (simulating handling conditions used in laboratory tests). Four wild captured larval red drum (~20 mm standard length) were placed in each pail and timed until death. Fish not used in experimental pails were left in the bucket in which they were transported (containing the uncontaminated water in which they were caught) to serve as controls. Effects of selected *P. brevis* cell concentrations on hatch rate and survival were tested by ANOVA following arcsine transformation of the percentage data to meet the assumptions of analysis of variance (Sokal and Rohlf 1981).

RESULTS

Peak densities of *P. brevis* occurred during 2-14 October 1986 (Fig. 2b). Although pier counts reached only 7,000 cells/ml, transient patches of *P.*

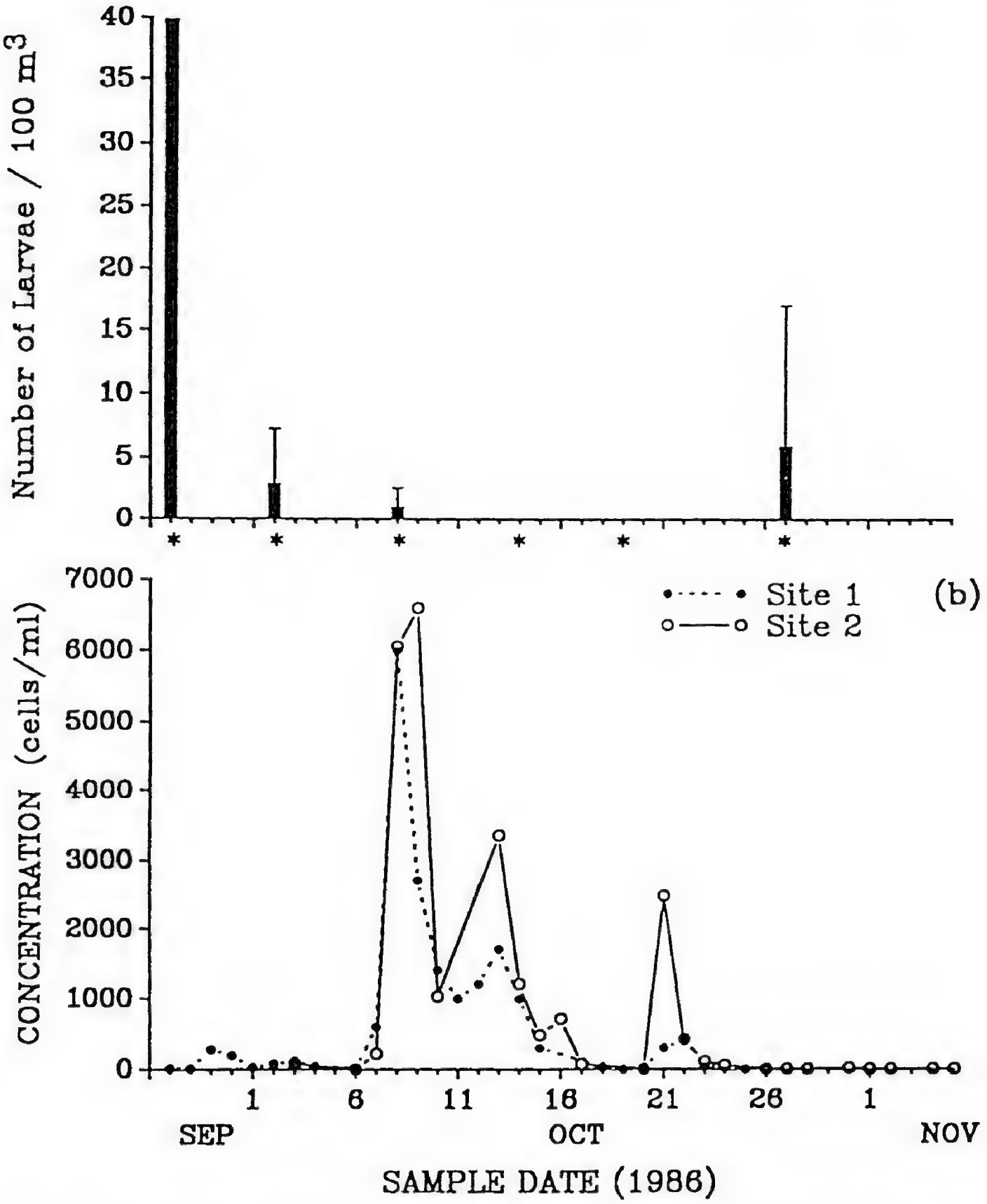


FIG. 2. (a) Density of red drum larvae (± 1 S.E.) in ichthyoplankton samples taken before, during, and after the 1986 red tide bloom (asterisks indicate days on which samples were collected) and

(b) population density of *P. brevis* at two sites in Port Aransas. Cell concentrations were derived from 3 replicate subsamples (0.1 ml) of a single large (5 L) water sample.

brevis in extremely high density (10,000-50,000 cells/ml) were commonly found in the surrounding area during the entire month of October, 1986.

The density of red drum larvae (Fig. 2a) was substantially lower following the onset of the red tide bloom than in the one ichthyoplankton sample taken prior to the bloom. Densities were at or near 0 during the height of the bloom but increased to more than 10/100 m^3 10 days after *P. brevis* cells were no longer found in water samples.

Hatch rates of red drum eggs (Fig. 3) exposed to red tide ranged from 96-100% and in all trials there were no significant differences between treated samples and controls (ANOVA $P > 0.05$). However, once hatched, larvae were negatively affected by all red tide concentrations $\geq$ 40 cells/ml (Fig. 3). In concentrations $\leq$ 23 cells/ml survival of larval red drum was not significantly different from controls but at all greater concentrations, mortality rates increased significantly (Table 1). Typically, all fish exposed to any concentration of red tide appeared deformed, swam abnormally, and displayed other signs of stress before death. Only fish in controls appeared normal in our laboratory studies. Table 1 provides details of statistical tests concerning mortality in larval red drum exposed to *P. brevis* toxins.

Older larval fish (21-day-old red drum) were also negatively affected by all concentrations of *P. brevis* but survival times were longer than for newly hatched larvae (Table 2). In the highest concentration (2040 cells/ml)

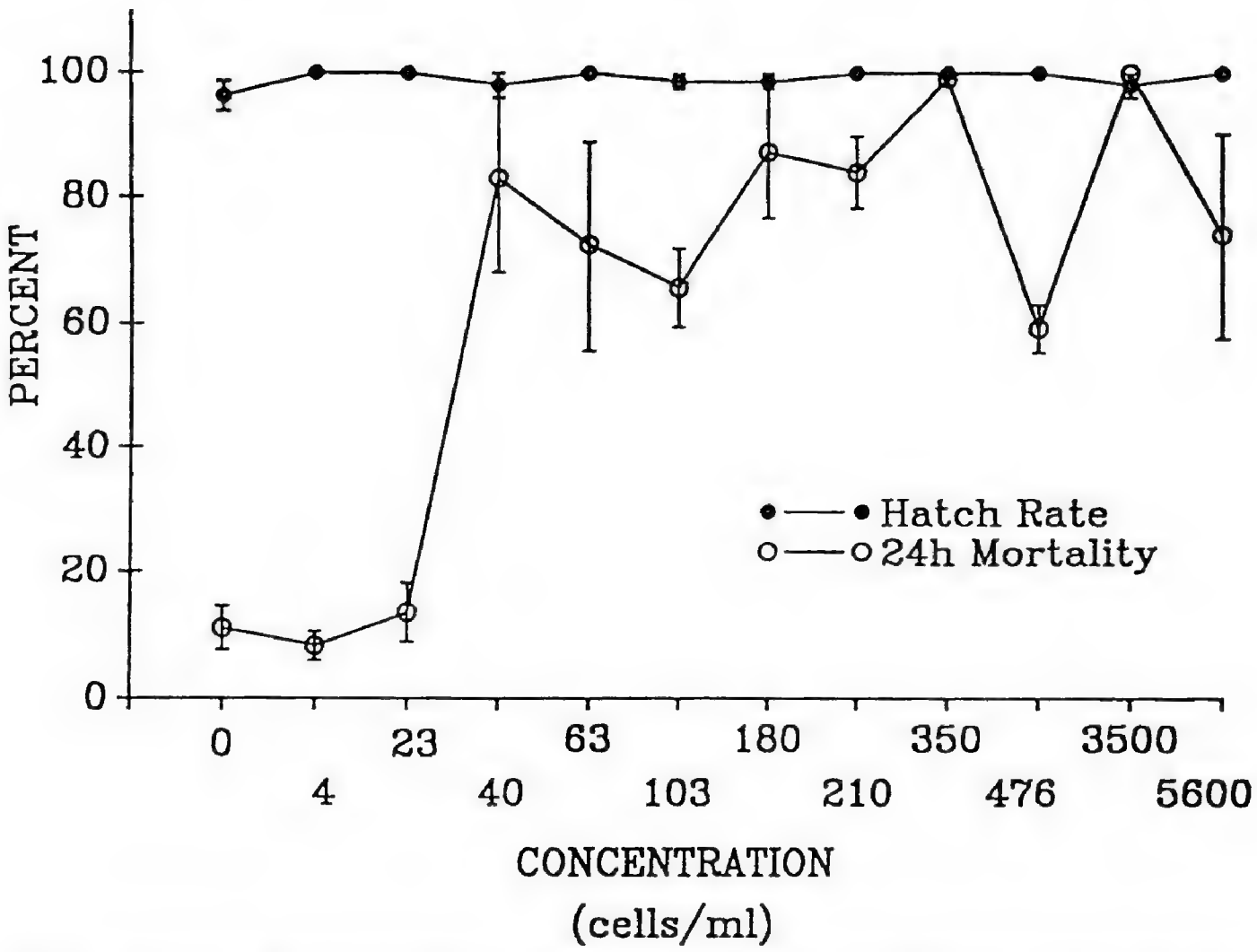


FIG. 3. Egg hatch rates and mortality rates (± 1 S.E.) of laboratory spawned red drum after 24 h exposure to increasing concentrations of *P. brevis*

TABLE 1

Percent mortality rates from three experiments with newly hatched larval red drum exposed to selected concentrations of *P. brevis* (cells/ml) during the first 24 hours after hatching.

	Concentration												Results of ANOVA			
Exp.	0	4	23	40	63	103	180	210	350	476	3500	35000	N	F	df	P
1	0	8	14	83	72								15	15.00	4,10	0.0003
2	13					66	87	84		59			15	10.60	4,10	0.0013
3	7								99		100	94	12	36.69	3, 8	0.0001

Values connected by lines are not significantly different (Tukey's Multiple Range Test).

TABLE 2

Mortality rates for 21-day-old red drum exposed to different concentrations of *P. brevis*. Where *N* = number of fish exposed to each concentration of *P. brevis* and mean mortality = the average number of minutes that elapsed until death occurred in each fish exposed to the same concentration of *P. brevis*. (Total exposure time = 48 hours.)

P. brevis Conc. (cells/ml)	Mean Mortality (Minutes)	N
33	1066	3
420	413	4
2040	72	2
controls	-	4

Total exposure time = 48h.

mortality occurred in ~1 h. In the lowest concentration (30 cells/ml) fish showed signs of stress (*i.e.*, abnormal swimming) after only 1 h of exposure but survived for ~15 hours. All fish in the controls survived and appeared normal throughout the entire 24 h observation period.

There was substantial variability in fish mortality rates in the higher *P. brevis* concentrations tested. To determine the influence of our handling techniques (*i.e.*, collection, transport, and handling of *P. brevis* cells) on experimental results we conducted field tests to see if fish mortality would be reduced if exposure occurred in a natural situation (*i.e.*, without disturbance of *P. brevis* cells). At the test site (*P. brevis* concentration = 47,680 cells/ml) there was a significant difference in mortality rates between larval red drum placed directly into the affected bay water ($\bar{x}$ death time = 114.3 min., N = 6) and those fish exposed to *P. brevis* bloom poured into the test buckets ($\bar{x}$ = 63.8 min., N = 8, ANOVA, P = 0.005, df = 12, F = 11.32).

DISCUSSION

The populations density of *P. brevis* was highly variable throughout the bloom period. The transient nature of the bloom due to tides and winds coupled with the fact that many marine dinoflagellates have the ability to migrate vertically resulted in highly variable cell counts between monitoring sites at any one time as well as significant diel variation at a site. Our counts may not accurately reflect the overall severity of the red tide outbreak since at any given time, some areas had high concentrations while in other areas they were low.

Toxins produced by *P. brevis* had no effect on egg hatch rates. Within egg membranes embryos are relatively well protected from their external environment. Conversely, larval fish are highly integrated with their environment and thus susceptible to red tide toxins. Not surprisingly, even very low concentrations of *P. brevis* were very toxic to newly hatched and one-day-old larval red drum. Larger larval fish and juveniles are more tolerant of toxins than newly hatched larvae, as evidenced by their increased survival time. It may be that larger fish are better able to escape exposure to toxins when environmental conditions allow for this (*i.e.*, bloom patches surrounded by unaffected water). It is also possible that as larval fish grow older they have greater potential for recovery. We have no direct data for this hypothesis; however, it would be an interesting topic for future research.

Field test results suggest that physical disturbance does increase the toxicity of *P. brevis* and as a result could have influenced survival time of fish in laboratory tests. However, both treatments resulted in 100% mortality of red drum and the mortality rates determined in the laboratory should not have been influenced by experimental procedures. Furthermore, naturally occurring disturbances (*i.e.*, wave action, currents) are always present so our laboratory procedures may be more realistic than the field test (conducted in calm water) would indicate.

The *P. brevis* bloom occurred after the peak of the red drum spawning period which occurs primarily in September. The decrease in density of larvae during the bloom was attributable to both toxic effects and the normal decrease in larval density as spawning activity diminishes. Nevertheless, the precipitous decline in numbers is certainly due in part to toxic effects which is corroborated by the increase in density following the bloom. The effect of the red tide bloom on the 1986 cohort of red drum in the Port Aransas area was minimal due primarily to two factors. First, substantial numbers of postlarvae reached the seagrass meadow nursery areas in September, prior to the bloom (and some possibly survived during the bloom). Second, preliminary analysis of concurrent studies showed that demersal postlarvae in seagrass meadows were killed only by "direct hits" of a bloom. Due to the patchy nature of blooms within the estuary, large segments of the shallow seagrass meadows were not directly impacted by the red tide, thus allowing survival of significant numbers of red drum postlarvae.

ACKNOWLEDGMENTS

Partial funding for this research was provided by Texas Advanced Technology Research Program. Special thanks go to Liz Young-Able who separated and identified larval fish from ichthyoplankton samples. We also thank Tony Amos, Sherrie Hatch and Gilbert Ramos for data collection and laboratory assistance and Pat Brown for preparing the map in Figure 1.

LITERATURE CITED

ARNOLD, C.R., W.H. BAILEY, T.D. WILLIAMS, A. JOHNSON and J.L. LASSWELL. 1977. Laboratory spawning and larval rearing of red drum and southern flounder. *Proceedings of the Annual Conference of the Southeastern Association Fish and Wildlife Agencies.* 31:437-440.

DUGDALE, R.C. 1979. Primary nutrients and red tides in upwelling regions, pp. 257-262. In Dennis L. Taylor and Howard H. Seliger (eds) *Toxic Dinoflagellate Blooms.* Elsevier North Holland, Inc.

HADDAD, K.D. and K.L. CARDER. 1979. Oceanic intrusion: one possible initiation mechanism of red tide blooms on the west coast of Florida, pp. 269-274. In Dennis L. Taylor and Howard H. Seliger (eds) *Toxic Dinoflagellate Blooms.* Elsevier North Holland, Inc.

HUNTLEY, M.E. 1982. Yellow water in LaJolla Bay, California, July 1980. II Suppression of zooplankton grazing. *Journal of Experimental Marine Biology and Ecology.* 63:81-91.

_____, P. SYKES, S. ROHAN and V. MARIN. 1986. Chemically medicated rejection of dinoflagellate prey by the copepods *Calanus pacificus* and *Paracalanus parvus*: mechanism, occurrence and significance. *Marine Ecology - Progress Series.* 28:105-120.

HURLBERT, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs.* 54:187-211.

ROBERTS, B.S., G.E. HENDERSON and R.A. MEDLYN. 1979. The effect of *Gymnodinium breve* toxin(s) on selected mollusks and crustaceans, pp. 419-424. In Dennis L. Taylor and Howard H. Seliger (eds) *Toxic Dinoflagellate Blooms.* Elsevier North Holland, Inc.

ROUNSEFELL, G.A. and W.R. NELSON. 1966. Red tide research summarized to 1964 including annotated bibliography. U.S. Fish and Wildlife Service. *Special Scientific Report, Fisheries.* No. 535. 85p.

SELIGER, H.H., M.A. TYLER and K.R. McKINLEY. 1979. Phytoplankton distributions and red tides resulting from frontal circulation patterns, pp. 239-248. In Dennis L. Taylor and Howard H. Seliger (eds) *Toxic Dinoflagellate Blooms.* Elsevier North Holland, Inc.

SIEVERS, A.M. 1969. Comparative toxicity of *Gonyaulax monilata* and *Gymnodinium breve* to annelids, crustaceans, molluscs and a fish. *Journal of Protozoology.* 16:401-404.

SNIDER, R. (ed). 1986. Red tide in Texas: an explanation of the phenomenon. Texas A&M Sea Grant College Program. TAMU-SG-87-502. Texas A&M University, College Station, Texas.

SOKAL, R.S. and F.J. ROHLF. 1981. *Biometry.* Freemen, New York. 858 pp.

SPIKES, J.J., S.M. RAY, D.V. ALDRICH and J.B. NASH. 1968. Toxicity variations of *Gymnodinium breve* cultures. *Toxicon.* 5:171-174.

STEIDINGER, K.A. 1975. Basic factors influencing red tides, p. 153-162. In V.R. LoCicero (ed) *Proceedings of the First International Conference on Toxic Dinoflagellate Blooms*, November 1974, Boston, Massachusetts. Massachusetts Science and Technical Foundation, Wakefield, Massachusetts.

_____. 1983. A re-evaluation of toxic dinoflagellate biology and ecology, pp. 147-188. In Round/Chapman (eds) *Progress on Phycological Research*, Vol. 2. Elsevier Science Publishers.

_____ and E.A. JOYCE. 1973. Florida red tides. Florida Department of Natural Resources. *Educational Series.* No. 17. 26p.

_____ and R.M. INGLE. 1972. Observations on the 1971 summer red tide in Tampa Bay, Florida. *Environmental Letters.* 3:271-278.

WARDLE,W.J., S.M. RAY and A.S. ALDRICH. 1975. Mortality of marine organisms associated with offshore summer blooms of the toxic dinoflagellate *Gonyaulax monilata* Howell at Galveston, Texas. pp. 257-263. In V.R. LoCicero (ed) *Proceedings of the First International Conference on Toxic Dinoflagellate Blooms*, November 1974, Boston, Massachusetts. Massachusetts Science and Technical Foundation, Wakefield, Massachusetts.

WILSON, W.B. and S.M. RAY. 1956. The occurrence of *Gymnodinium brevis* in the western Gulf of Mexico. *Ecology*. 37:388.

Contributions in Marine Science. (1989) Vol. 31:147–161.

OCCURRENCE OF A DINOFLAGELLATE BLOOM ASSOCIATED WITH AN INFLUX OF LOW SALINITY WATER AT GALVESTON, TEXAS, AND COINCIDENT MORTALITIES OF DEMERSAL FISH AND BENTHIC INVERTEBRATES

Donald E. Harper, Jr. and George Guillen[1]

Texas A&M Marine Laboratory
5007 Avenue U
Galveston, Texas 77551

ABSTRACT

Low salinity water and an associated dinoflagellate bloom appeared suddenly off Galveston, Texas, in early June 1984. An aerial survey showed the bloom extended east at least as far as Cameron, Louisiana. High discharge from the Mississippi-Atchafalaya Rivers between March and late May, and a strong, wind-driven downcoast current preceded the appearance of low salinity water and its associated bloom. Within a week of the first appearance of the bloom, demersal fish, numerically dominated by Atlantic threadfin (*Polydactylus octonemus*) began dying early in the morning and washing ashore. Calm weather conditions occurred during the latter part of the kill and anaerobic silt accumulated on the bottom offshore from Galveston. We believe the kill was caused by hypoxia and/or hydrogen sulfide production resulting from nocturnal metabolism of the bloom and anaerobic decay of dead dinoflagellate cells. A second kill in mid-July, numerically dominated by Atlantic croaker (*Micropogonias undulatus*), was probably the bycatch or cull of shrimping vessels working offshore.

INTRODUCTION

Galveston experiences periodic blooms of phytoplankton (usually diatoms or dinoflagellates) in nearshore waters. Depending on the size and composition of the bloom, the organisms may do little more than cause nocturnal phosphorescence (*i.e., Gonyaulax, Noctiluca*) or the bloom may be associated with mortalities of fish and invertebrates. Mortalities may be caused by toxins produced by the plankters; the "red tide" organism, *Ptychodiscus (=Gymnodinium) brevis* has long been known to be associated with fish kills in Florida (Rounsefell and Nelson 1966, Joyce 1975, LoCicero 1975, Taylor and Seliger 1979) and was responsible for fish kills along the Texas coast in 1955 (Wilson and Ray 1956) and in 1986-87 (Trebatoski 1988, unpublished data).

---

[1] Present address: Texas Water Commission, Deer Park, Texas 77536

Wardle, Ray and Aldrich (1975) reported "red tides" at Galveston in 1971 and 1972 caused by blooms (up to 1.88×10^6 cells/l) of *Gonyaulax monilata*. Mortalities of benthic macroinvertebrates and a few benthic fish were attributed to toxins produced by the bloom.

Another cause of mortalities of fish and invertebrates is the creation of hypoxic (< 2.0 ppm O_2) or anoxic conditions in the water column. These conditions may result from oxygen being consumed by combined metabolic activities of large blooms at night (especially prevalent in confined channels (Knudsen and Bellaire 1975)) or by death and bacterial decomposition of large blooms (Griffiths, Dennis and Potts 1979; Forster 1979; Swanson and Sindermann 1979; Garlo, Milstein and Jahn 1979; Falkowski, Hopkins and Walsh 1980; Officer, Biggs, Taft, Cronin, Tyler and Johnson 1984; Taylor, Taylor and Walsby 1985). Prolonged anoxia may produce conditions in which sulfate reducing bacteria, normally found deeper in sediments, can survive at or near the mud-water interface (Jørgensen 1980). These organisms produce hydrogen sulfide and can accelerate mortalities among bottom dwelling organisms (Brongersma-Sanders 1957). Widespread benthic mortalities and low nekton catches off Freeport, Texas, in 1979 were associated with a stratum of hydrogen sulfide-laden water above the bottom (Harper, McKinney, Salzer and Case 1981; Pavella, Ross and Chittenden 1983). Hydrogen sulfide was also implicated in extensive mortalities in Chesapeake Bay in 1984 (Seliger, Boggs and Biggley 1985) and suspected in a New Zealand kill (Taylor, Taylor and Walsby 1985).

Hypoxia is relatively common offshore from Louisiana (Gaston 1985; Gaston, Rutledge and Walther 1985; Boesch 1985; Rabalais, Dagg and Boesch 1985; Pokryfki and Randall 1987), but apparently occurs rarely off the Texas coast (Harper *et al.* 1981, Rabalais *et al.* 1985). Available data indicate that hypoxia in the northern Gulf of Mexico is usually associated with high river discharge, a phytoplankton bloom, and stratification of the water column due to calm weather and/or strong temperature-salinity gradients (Gunter 1979; Harper *et al.* 1981; Boesch 1985; Rabalais *et el.* 1985; Pokryfki and Randall 1987). The principal source of low salinity water along the upper Texas coast is combined discharge from the Mississippi-Atchafalaya River; local discharge generally results in only localized salinity reductions offshore (Kelly, Schmitz, Ulm, Randall and Cochrane 1985a). The local wind regime causes a predominantly westward current (Pokryfki and Randall 1987; Cochrane and Kelly 1986) and 1.5 to 2 months usually elapse between peak Mississippi-Atchafalaya discharge and the occurrence of lower salinity water off the upper Texas coast (Temple, Harrington and Martin 1977).

A trait of many phytoplankton blooms is that they appear "suddenly" and by the time researchers begin to investigate a bloom, it is well developed. Consequently it is often difficult to determine if the bloom was initiated locally or if it was transported from elsewhere, and to hindcast events preceding and causing the bloom. In the present study we were fortunate to have been participating in a research project in which hydrographic data were being gathered upcoast and downcoast from Galveston at the same time a bloom

appeared suddenly at Galveston in June 1984. We believe we were able to correlate this bloom with movement of a water mass, and its already developed bloom, into Texas from Louisiana. The main concern of this paper is not with the bloom *per se*. Rather we attempt to correlate hydrographic data with the occurrence of the bloom and hindcast a sequence of events that lead to the appearance of the bloom at Galveston.

METHODS

Various qualitative observations were made throughout the duration of the phytoplankton bloom and associated fish kill between 9 and 30 June 1984, and a second fish kill in mid-July 1984. An aerial survey was made along the shoreline between Cameron, Louisiana, and East Matagorda Bay, Texas, on 19 June to determine the horizontal and lateral extent of the bloom (Fig. 1). On 21 June visual observations and hydrographic measurements were made during a cruise along a transect between Cameron and Galveston (Fig. 1). Beach water temperature, salinity and dissolved oxygen (D.O.) were measured periodically at Galveston throughout the bloom. Wind and current data gathered 8 km off Cameron, Louisiana, and 19 km off Freeport, Texas, by Kelly *et al.* (1985a, b) were examined to determine the physical factors which may have preceded the observed phenomenon.

Mortalities were estimated at several localities along the upper Texas coast (Fig. 2) according to established American Fisheries Society guidelines (Pollution Committee 1982). The expansion factor used to estimate dead organisms was:

$$\frac{\text{km of beach affected} \times 1000 \times \text{fish counted}}{\text{Sum length of transects (m)}}$$

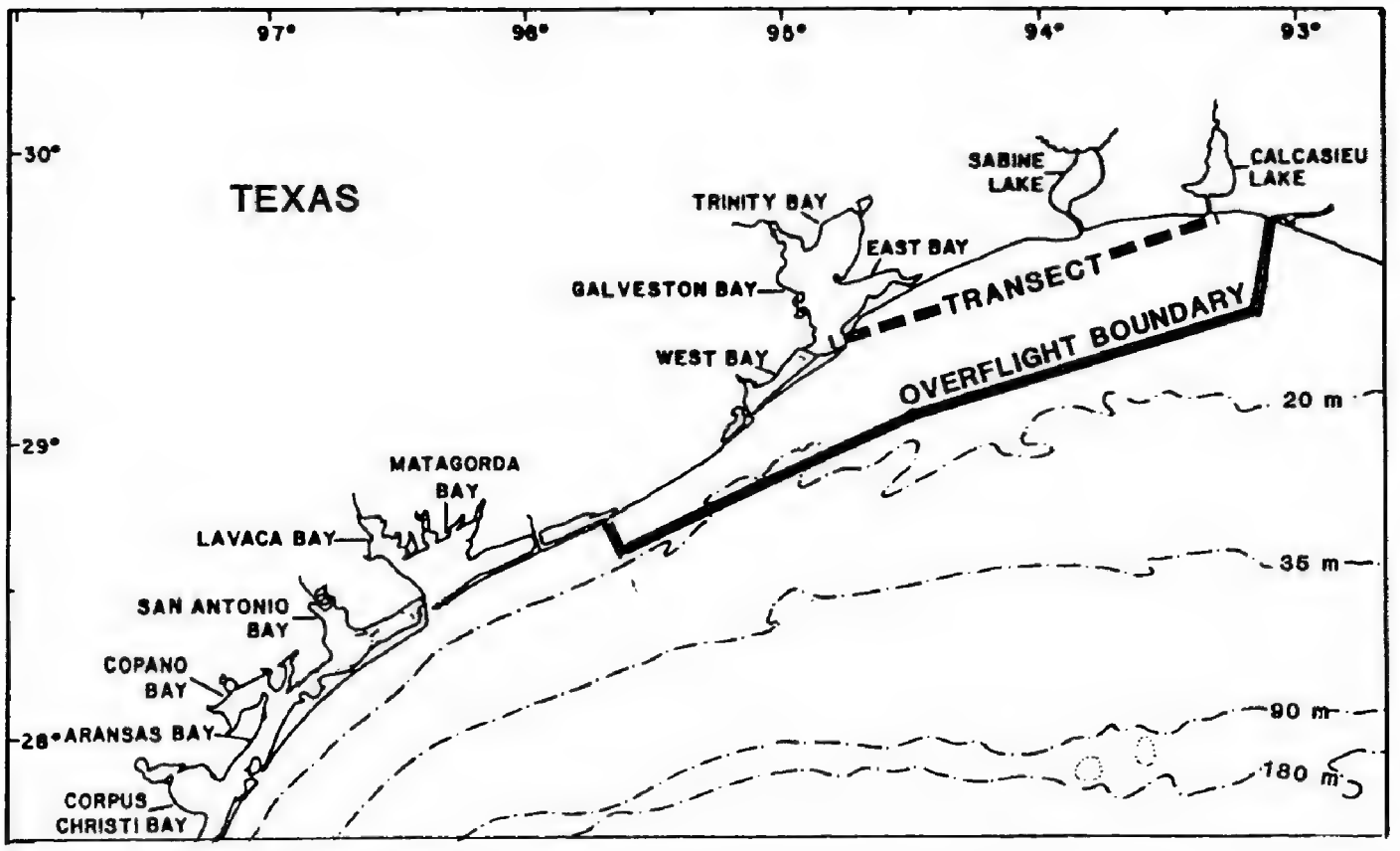


FIG. 1. Map of the northwestern Gulf of Mexico showing the approximate area of coverage of the dinoflagellate bloom as determined by overflight and cruise observations.

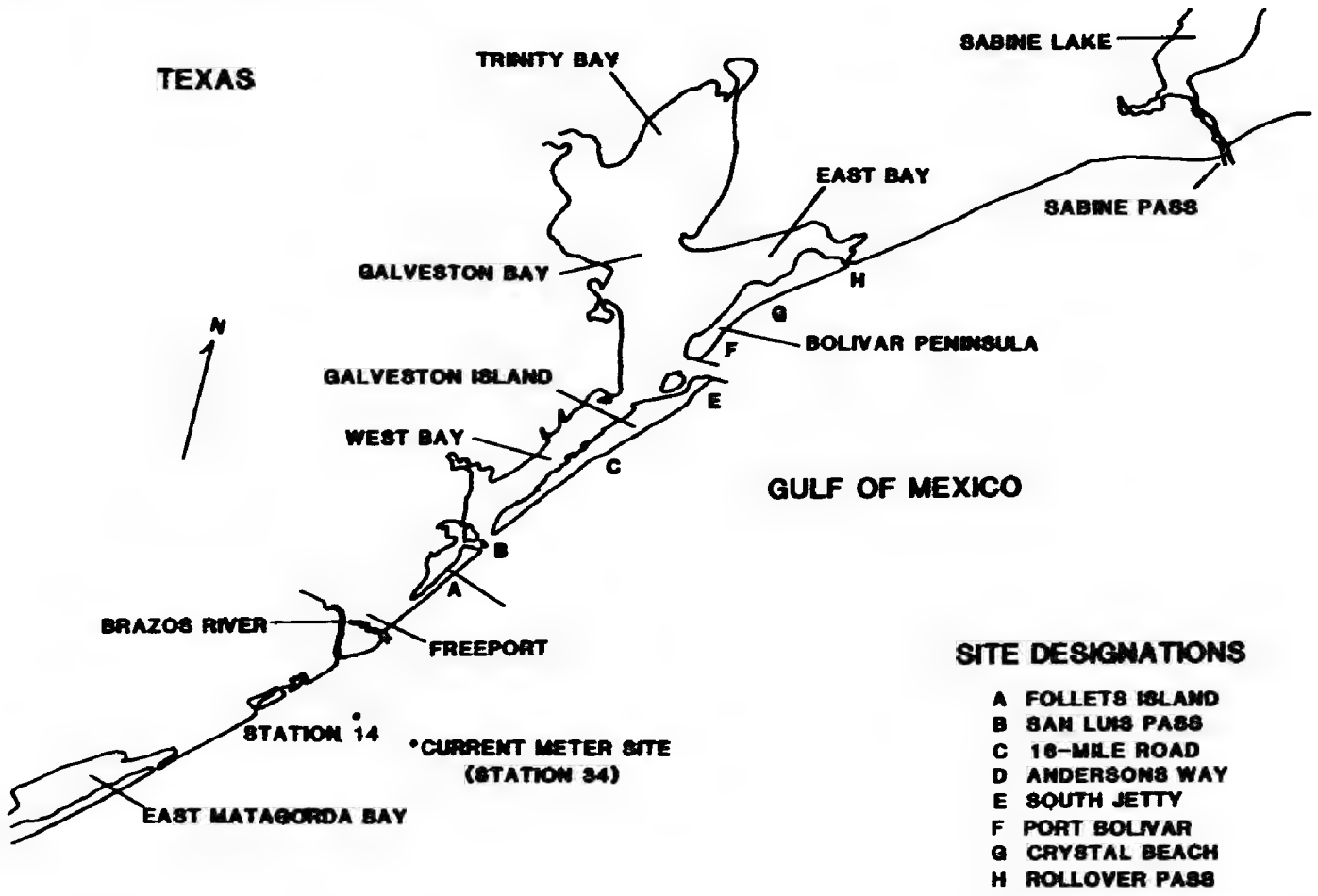


FIG. 2. Map of the upper Texas coast showing locations of beaches surveyed for abundances of dead organisms (listed in Tables 1 and 2). Also shown are locations of the current meter off Freeport (Station 34) and an inshore hydrographic sampling station (14).

Aerial surveys of the entire Galveston Bay complex and Gulf beaches between Rollover Pass and San Luis Pass were made on 20 and 29 June. Other information on the extent of the kill was provided by state and federal biologists in Texas and Louisiana. Estimates of commercial fishing pressure were made throughout the bloom's duration.

A second fish kill, first reported on 10 July 1984, extended through at least 11 July. Dead fish were observed floating and stranded in some of the general areas affected during the 21-27 June kill, and were censused at several of the same localities censused in June. Qualitative observations were made on commercial fishing pressure and presence of dead fish from High Island to Freeport. An aerial survey of the Galveston Bay complex and Gulf beaches was conducted on 11 July 1984.

RESULTS

General Observations

The first indication of unusual water conditions at Galveston occurred between 9 and 10 June, 1984; the water was relatively clear on 9 June, but on the 10th the bloom was present and colored the water brown to reddish brown (this coloration was associated with a mucoid or slimy sensation when the water was touched). From 11 through 14 June the bloom formed a brown band about 10 m wide very close to the beach and was associated with a strong odor of algae. A water sample collected on 14 June contained several species of dinoflagellates with *Gymnodinium splendens* as the numerical dominant

(Laurel Loeblich personal communication). Attempts at culturing these dinoflagellates were unsuccessful, but survival did appear to be greater at lower salinities. On 15 June the bloom had moved 10-15 m offshore from the beach and remained offshore thereafter at Galveston.

The aerial survey on 19 June revealed that brown water occurred from the southwest end of Galveston Island east to at least Cameron, Louisiana. Near passes to bay systems, the bloom formed large patches along convergence lines. Between bay entrances the bloom frequently formed long, regularly spaced parallel lines, suggesting concentration by Langmuir circulation. Overall, the brown water varied from being restricted very close to the beach to extending an estimated 10 km offshore. Numerous menhaden fishing vessels were observed working rather close to shore west of Cameron, and nearly all were fishing in or near patches of brown water. Shrimping vessels, however, were not working in these regions.

On 21 June observations and hydrographic measurements were made along a transect between Cameron and Galveston (Fig. 1). A few parallel brown streaks, first noted in the Sabine Pass area, became more numerous to the west. Large patches of brown water were first encountered offshore from Rollover Pass, Texas, and continued to Galveston. A plankton tow was attempted in one patch (29°25.5′ N, 94°27.0′ W) and the net became clogged in about 10 seconds. The plankton sample contained large numbers of *Gymnodinium splendens*.

Hydrographic Conditions

The bloom was associated with low salinity water. This water mass was at least initially restricted to a narrow band close to the beach (hence the brown water close to shore). On 14 June a water sample collected at the beach had a salinity of 9‰, but 21.4‰ was recorded by the National Ocean Survey (NOS) at the end of the Galveston Pleasure Pier, 300 m from shore (Fig. 3). On 18 June the beach water salinity had increased to 15‰ while the salinity recorded by NOS was 22.4‰ (Fig. 3). Salinities recorded by NOS did not decrease below 20‰ until 19 June, and never got below 16‰ (21 June).

On 21 June, during the cruise from Cameron to Galveston, a pronounced oxycline was found at 4- to 5-meter depths between Cameron and Sabine Pass (Texas-Louisiana border); the water column was hypoxic below these depths. Hydrographic data west of Sabine Pass are not available due to meter malfunction.

Winds were calm during 23 through 26 June, and the beach water at Galveston became quite clear by 25 June as suspended material settled. Water temperature, salinity and D.O. measured at mid-afternoon (1500 hours) in the surf zone at west Galveston Island on 23 June were 32°C, 25‰ and 5.2 ppm, respectively. On 26 June at 0600 hours, beach water temperature, salinity and D.O. ranged from 28.0-28.5°C, 28.0-30.0‰ and 5.0-6.0 ppm, respectively, between Galveston Bay entrance and the west end of the Galveston seawall.

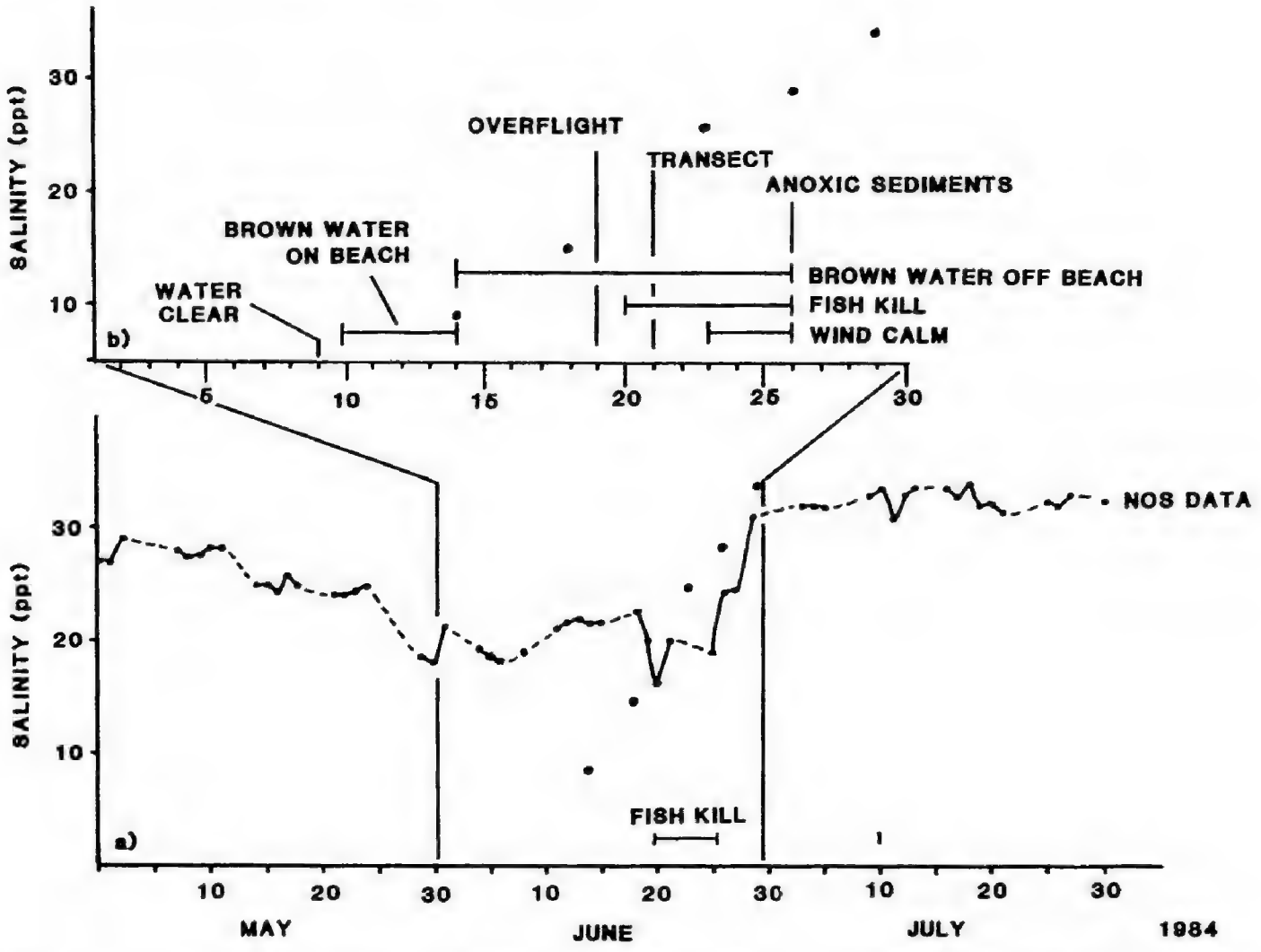


FIG. 3. (a) Chronology of events at Galveston, Texas, May - July 1984, before, during and after occurrence of mortalities. (b) Details of events in June 1984. Individual dots represent surf zone salinities measured at Galveston. NOS data recorded about 300 m off the beach at the Galveston Pleasure Pier.

Also on 26 June at 1600 hours, a 4-6 cm thick layer of black, hydrogen sulfide-laden, anaerobic silt was found covering the sandy bottom 200 m offshore at Galveston. The salinity and D.O. of a water sample collected just above the bottom were 29.5‰ and 5.0 ppm, respectively. An attempt to resample the same locality at 0600 hours the following day, when D.O. should have been lowest, was canceled because an onshore wind had arisen, creating choppy water conditions. The water column was apparently being agitated because the wind carried a strong smell of decaying algae-hydrogen sulfide.

On 29 June the surface salinity in the Galveston Channel was 34‰. The bottom water dissolved oxygen was 2.5 ppm. There was no evidence of discolored water.

Mortalities

Texas Parks and Wildlife Department (TPWD) records indicate large numbers of dead fish stranded on Texas beaches between Freeport and Galveston in the early day light hours of 20 and 22 June 1984. Reports indicate

that dead fish appeared to float and begin to strand almost simultaneously throughout the affected area. Atlantic threadfin (*Polydactylus octonemus*), Atlantic croaker (*Micropogonias undulatus*) and southern kingfish (*Menticirrhus americanus*) numerically dominated concentrations of stranded organisms on the beaches between Rollover Pass and Freeport (Table 1); Atlantic threadfin accounted for 79% of the total number. Other surveys conducted by federal and state biologists revealed that the kill extended from Sabine Pass to about Freeport, Texas, (Fig. 2), and that Atlantic threadfin also numerically dominated concentrations of dead fish observed on these beaches. Neither dead fish nor brown water were ever seen within any bay system.

As mentioned previously, commercial menhaden vessels were observed fishing in or near patches of brown water west of Cameron, Louisiana, during the aerial survey on 19 June. TPWD data indicate little commercial shrimping activity was recorded from 18 through 29 June; only 7 and 14 shrimp boats were observed operating on 20 and 29 June, respectively, between Rollover Pass and Port Bolivar. Few shrimping vessels were seen during the beach surveys where dead fish were being counted.

TABLE 1

Total estimated number of dead organisms found on Gulf beaches between Sabine Pass and San Bernard Wildlife Refuge during 23 June and 25 June 1984. A 13.7 meter sampling transect was used at Station A; 2.7 meter transects were used at remaining stations. Size ranges are standard lengths except for *Callinectes sapidus*.

Species	Size Range	Station count - Number of Organisms/2.7 meters						Estimated			
		A	B	C	D	E	F	Mean	Total Number	±	2SE
Crustacea											
Callinectes sapidus	7.5-17.5	0.2	--	--	3.0	8.0	--	1.9	113,459	±	155,392
Pisces											
Brevoortia patronus	5.0	--	--	--	--	--	1.0	0.2	10,130	±	15,694
Opisthonema oglinum	12.5	--	--	--	--	--	1.0	0.2	10,130	±	15,694
Anchoa mitchilli	5.0	0.2	--	--	--	--	--	<0.1	2,026	±	3,139
Arius felis	22.5-30.0	0.4	--	--	--	--	1.0	0.2	14,182	±	18,569
Menidia beryllina	7.5	--	--	--	1.0	--	--	0.2	10,130	±	22,194
Pomatomus saltatrix	25.5	--	--	--	--	1.0	--	0.2	10,130	±	22,194
Chloroscombrus chrysurus	13.0	0.2	--	--	--	--	--	<0.1	2,026	±	3,139
Bairdiella chrysoura	2.5-10.0	2.0	2.0	--	--	--	1.0	0.8	50,651	±	35,092
	12.5-20.0	0.6	7.0	--	1.0	--	--	1.4	87,120	±	149,676
								2.3	137,771	±	174,729
Cynoscion arenarius	7.5	--	--	--	--	--	1.0	0.2	10,130	±	15,694
Leiostomus xanthurus	10.0	--	1.0	--	--	--	1.0	0.3	20,260	±	27,182
Menticirrhus americanus	10.0	2.0	1.0	--	--	--	--	0.5	30,391	±	22,194
	12.5-20.5	50.0	27.0	--	13.0	--	1.0	15.2	921,852	±	627,160
	23.0-35.5	1.6	6.0	2.0	--	--	--	1.6	97,250	±	98,458
								17.3	1,049,493	±	646,909
Micropogonias undulatus	5.0-10.0	--	2.0	--	6.0	--	114.0	20.3	1,235,890	±	1,794,582
	12.5-20.0	0.6	2.0	--	--	1.0	--	0.6	36,469	±	44,277
								20.9	1,272,359	±	1,779,529
Chaetodipterus faber	5.0-15.0	0.4	4.0	--	--	--	--	0.7	44,573	±	84,455
Mugil cephalus	18.0-25.0	--	3.0	--	1.0	--	--	0.7	40,521	±	70,184
Polydactylus octonemus	7.5-15.0	433.0	466.0	82.0	24.0	--	17.0	170.3	10,353,116	±	6,134,095
Astroscopus y-graecum	10.0	--	--	--	1.0	--	--	0.2	10,130	±	22,194
Total	--	491.2	521.0	84.0	44.0	10.0	138.0	214.7	13,049,788	±	7,208,816

A second fish kill occurred on 10 July 1985. However, the extent and composition of the kill, and associated hydrologic characteristics, differed from those associated with the June kill. The July kill was limited to Gulf beaches between Rollover Pass and Freeport, lower numbers of dead organisms were observed compared to the June kill, and the distribution of these organisms was more patchy and uneven than during the June incident. Concentrations of dead organisms were numerically dominated by Atlantic croaker (*Micropogonias undulatus* (Table 2), and the majority of dead fish were generally larger (>15 cm) than those observed during the June kill (<15 cm). No dead fish or patches of discolored water were seen within Galveston Bay entrance or any of the adjoining bays.

Windy weather and choppy brown turbid water occurred during the July kill, and large numbers of shrimp boats were operating. Two to five shrimp boats/km were observed operating offshore in localities where dead fish counts were being conducted. During an aerial survey on 11 July, 79 shrimp boats were observed working an area off the beaches near Rollover Pass.

DISCUSSION

The only area where hypoxic oxygen levels were recorded during this study was off Louisiana; D.O. values were less than 2.0 ppm below a pronounced oxycline at 4- to 5-m depth. None of the D.O. determinations were made at night or in deeper water. Despite the fact that all D.O. concentrations

TABLE 2

Total estimated number of dead organisms found on Gulf beaches between Rollover Pass and Freeport during 10 and 11 July 1984. A 13.7 meter sampling transect was used at Station F; 91.4 meter transects were used at remaining stations. Size ranges are standard lengths except for *Callinectes sapidus*.

Species	Size Range	Station Count - Number of Organisms/2.7 meters							Mean	Estimated Total Number	±	2SE
		D	E	F	G	H1	H2	H3				
Crustacea												
Callinectes sapidus	10.0-15.0	0.03	--	--	--	0.06	--	0.03	0.01	592	±	715
Pisces												
Rhizopriodon terraenovae	30.5-40.6	--	--	--	--	0.12	--	--	0.02	592	±	1,278
Arius felis	10.0-45.5	--	--	0.39	0.12	0.09	0.23	0.35	0.17	6,657	±	4,072
Chloroscombrus chrysurus	10.0-20.0	0.15	--	0.20	--	0.15	0.06	0.12	0.10	3,353	±	3,166
Decaptunus punctatus	23.0	0.03	--	--	--	--	--	--	<0.01	148	±	256
Trachinotus carolinus	35.5	--	--	--	--	--	0.03	--	<0.01	148	±	320
Bairdiella chrysoura	15.0	--	--	--	--	--	0.03	--	<0.01	148	±	320
Cynoscion arenarius	10.0-15.0	--	--	0.39	0.03	--	--	--	0.06	2,071	±	4,004
Cynoscion nebulosus	35.5-45.5	--	--	--	--	0.03	--	0.05	0.01	394	±	494
Leiostomus xanthurus	10.0	--	--	0.20	--	--	--	--	0.03	986	±	2,131
Mentricirrhus americanus	20.5-41.0	0.03	--	--	--	0.15	0.12	0.20	0.07	2,466	±	1,643
Micropogonias undulatus	5.0-10.0	--	--	8.30	0.17	--	--	--	1.21	41,767	±	87,525
Chaetodipterus faber	10.0-35.5	--	--	--	--	0.03	0.03	--	0.01	296	±	320
Mugil cephalus	10.0-45.5	--	0.09	0.20	--	0.23	0.58	0.81	0.27	9,419	±	5,737
Polydactylus octonemus	7.5-12.5	--	--	0.79	--	--	--	--	0.11	3,896	±	8,416
Balistes capriscus	10.0	--	--	--	--	0.03	--	--	<0.01	148	±	320
Reptilia												
Lepidochelys kempii	23.0	--	--	--	0.03	--	--	--	.01	148	±	320
Total		0.24	0.09	10.47	0.35	0.89	1.23	1.56	2.12	73,130	±	109,419

recorded at Galveston were above hypoxic levels, we believe mortalities of fish and invertebrates during late June 1984 were probably due to hypoxia and/or hydrogen sulfide, not dinoflagellate toxicity or commercial fishing activities. A number of factors support this conclusion. First, the dominant phytoplankter observed during the bloom, *Gymnodinium splendens* is not known to produce a lethal toxin (Laurel Loeblich personal communication), and has been used as a laboratory food for anchovy (*Engraulus mordax*) larvae (Eppley and Harrison 1975) and copepods (Paffenhofer 1970; Esaias and Curl 1972) (although Fiedler 1982 found that macrozooplankton actively avoided a dense layer of *G. splendens*, and filtration rates of herbivorous copepods were significantly reduced within this layer). Second, the majority of organisms killed were demersal fish and benthic invertebrates, and a dinoflagellate toxin would be expected to kill more species. Third, planktivorous Gulf menhaden (*Brevoortia patronus*) were apparently feeding in patches of phytoplankton, because commercial fishing boats were observed concentrating their efforts within these patches. If the dinoflagellates were producing toxin, the menhaden would probably have either avoided water masses with high densities of plankton, or been killed and observed floating on the surface. In either case, the boats would have been fishing elsewhere. Fourth, black anaerobic silt covering the sand bottom at Galveston in June indicated a build-up of hydrogen sulfide which probably resulted from decay of phytoplankton cells settling to the bottom during the calm weather period in June.

The appearance of the bloom in Galveston can probably be attributed to two major factors, *i.e.* very high river discharge (thus high nutrient concentrations) and wind conditions that concentrated the bloom along the coast, then caused rapid transport into Texas via a strong alongshore current.

Combined Mississippi-Atchafalaya discharge was quite large in the spring of 1984 and extended from March through mid-June (Kelly *et al.* 1985a). Three distinct peak flows occurred, in March (*ca.* 35,000 m^3/sec), in mid-April (*ca.* 44,000 m^3/sec) and in late May (*ca.* 48,000 m^3/sec). We believe water discharged in the second (or third) peak was the source of low salinity water associated with the dinoflagellate bloom because of the rate of westward transport. Data recorded at Galveston suggest that the low salinity water was initially close to the coast. The salinity meter off Cameron recorded two low salinity pulses, one in mid-May and one on 8 June (Fig. 4); this latter pulse was recorded two days prior to the appearance of low salinity water at Galveston. The mid-May, but not the June, pulse was also recorded by the meter off Freeport. The June pulse was, however, recorded closer to shore during routine hydrographic measurements made off Freeport. Two stations, 14 and 34 (8 and 19 km offshore, respectively) (Fig. 2), were part of a hydrographic transect that extended offshore from Freeport (Kelly *et al.* 1985a). Comparative time-depth plots of salinity for these two stations show a strong influx of fresher water in June that lowered the salinity at station 14 to about 17‰ (Fig. 5), while the salinity at station 34 remained high.

Cochrane and Kelly (1986) stated that there is strong coherence between wind and current direction along the northern Gulf of Mexico coast. Rapid

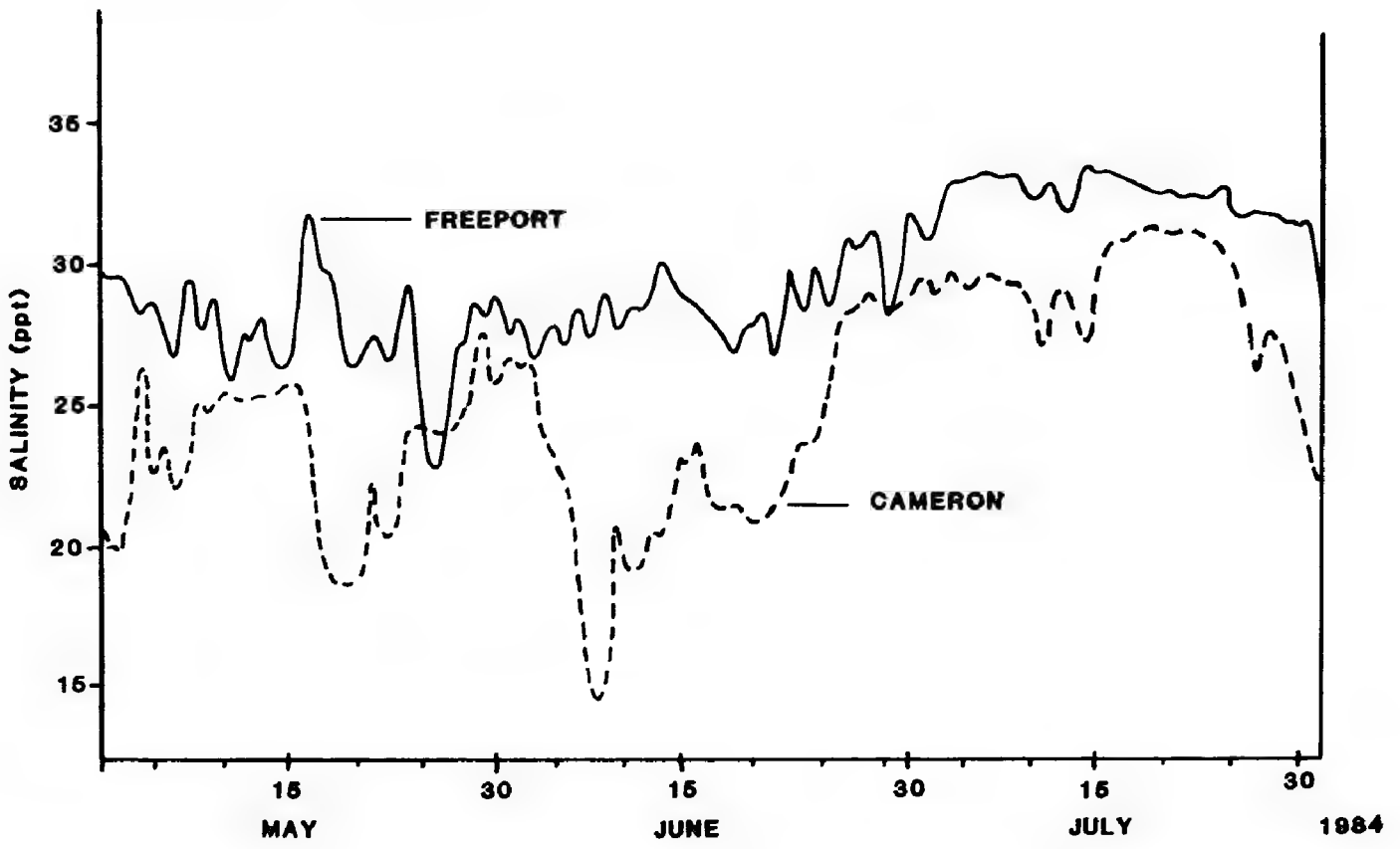


FIG. 4. Daily salinity records from surface meters located off Cameron, Louisiana, and Freeport, Texas (from Kelly *et al.* 1985 a,b).

advection of low salinity water from Louisiana into Texas may be explained by wind and current data gathered off Cameron, Louisiana, and Freeport, Texas (Kelly *et al.* 1985a,b). Mean winds and surface currents were downcoast (westward) and onshore during the spring (Fig. 6), which produced downwelling of surface water and kept fresher water adjacent to the coastline. Daily wind and current speed and direction data from Freeport indicated that while mean surface current flow was downcast in March and April, there were frequent current reversals which would have slowed net transport toward the Texas coast. In May and through mid-June, surface current flow was almost continually downcoast; between 23 May and 11 June, speeds were mostly between 30 to 60 cm/sec, which would have carried water from Cameron to Galveston (150 km) in 2.8 to 5.7 days. A switch from a downcoast, onshore current to an upcoast, offshore current was recorded on 20 June, 5 days after the bloom was observed to have moved away from the beach at Galveston. This current flow, which would cause an upwelling condition and move higher salinity water from offshore toward the coast, persisted until 11 July, the period of time in which beach water salinities rapidly increased into the 30‰ range.

Evidence of downcoast currents is also present in cross-shelf salinity profiles (which correspond almost exactly with sigma-t isopleths) reported by Kelly *et al.* (1985a,b) (Fig. 6). On 15 May isohalines were slightly tilted toward the coast of Freeport, indicating slight downcoast current. On 30 May at Cameron and on 11 June at Freeport, strongly tilted isohalines indicated a strong pressure gradient producing rapid downcoast current flow. On 20

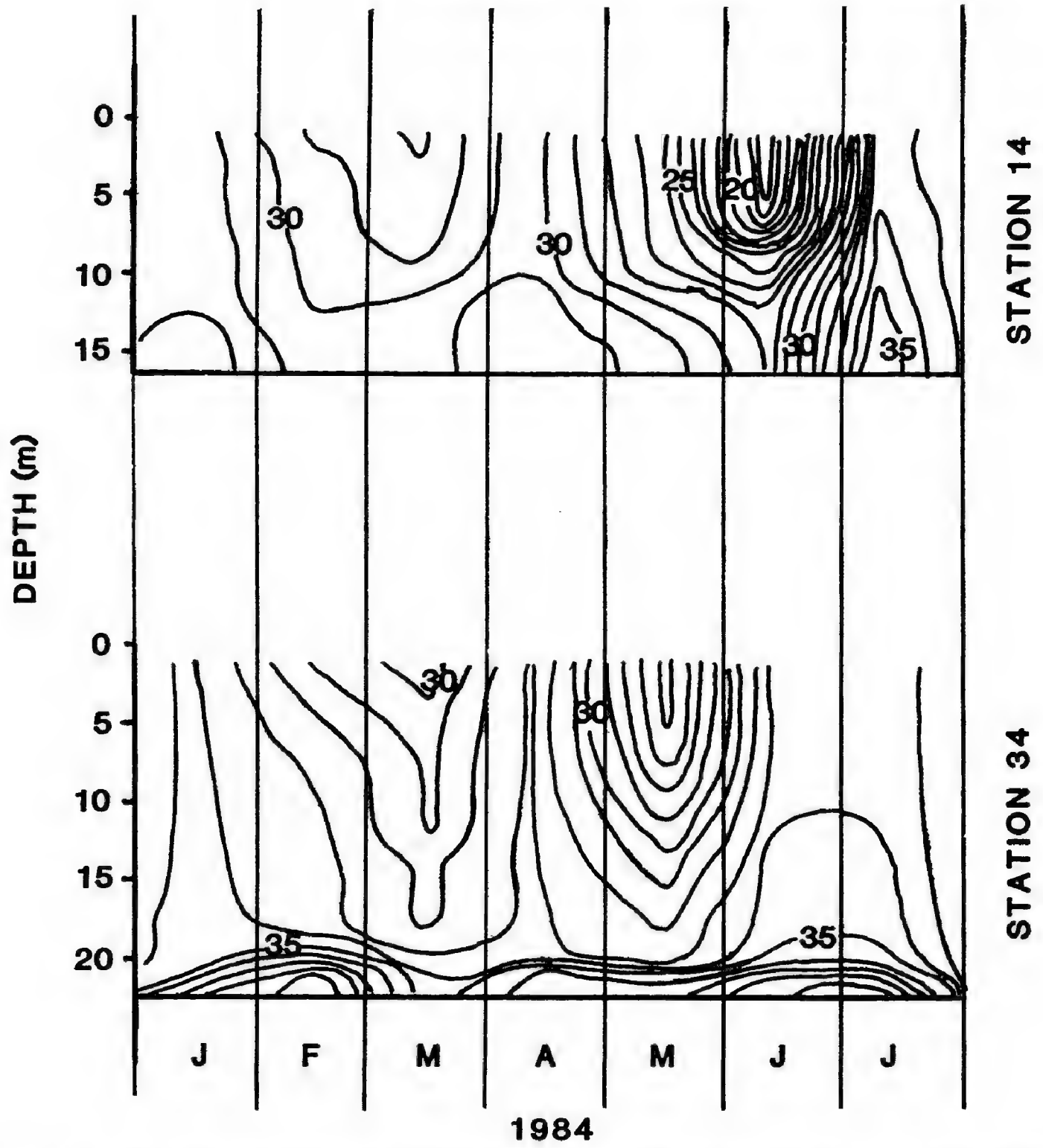


FIG. 5. Time-depth plots of salinity recorded at stations 14 and 34 off Freeport, Texas (from Kelly *et al.* 1985a).

June, after the winds had shifted to upcoast and offshore, isohalines at Cameron were nearly horizontal.

Another possible cause of the observed kills is commercial fishing activity. Large numbers of demersal fish comprised the bycatch or cull of commercial shrimping operations (Bryan, Cody and Matlock 1982). Small patches of floating dead fish culled from shrimp boats occur intermittently throughout Texas bays and nearshore waters. Commercial shrimping activity was relatively low during the June kill and very high during the July incident. During the July kill, dead organisms occurred in smaller numbers within a smaller area and were numerically dominated by Atlantic croaker

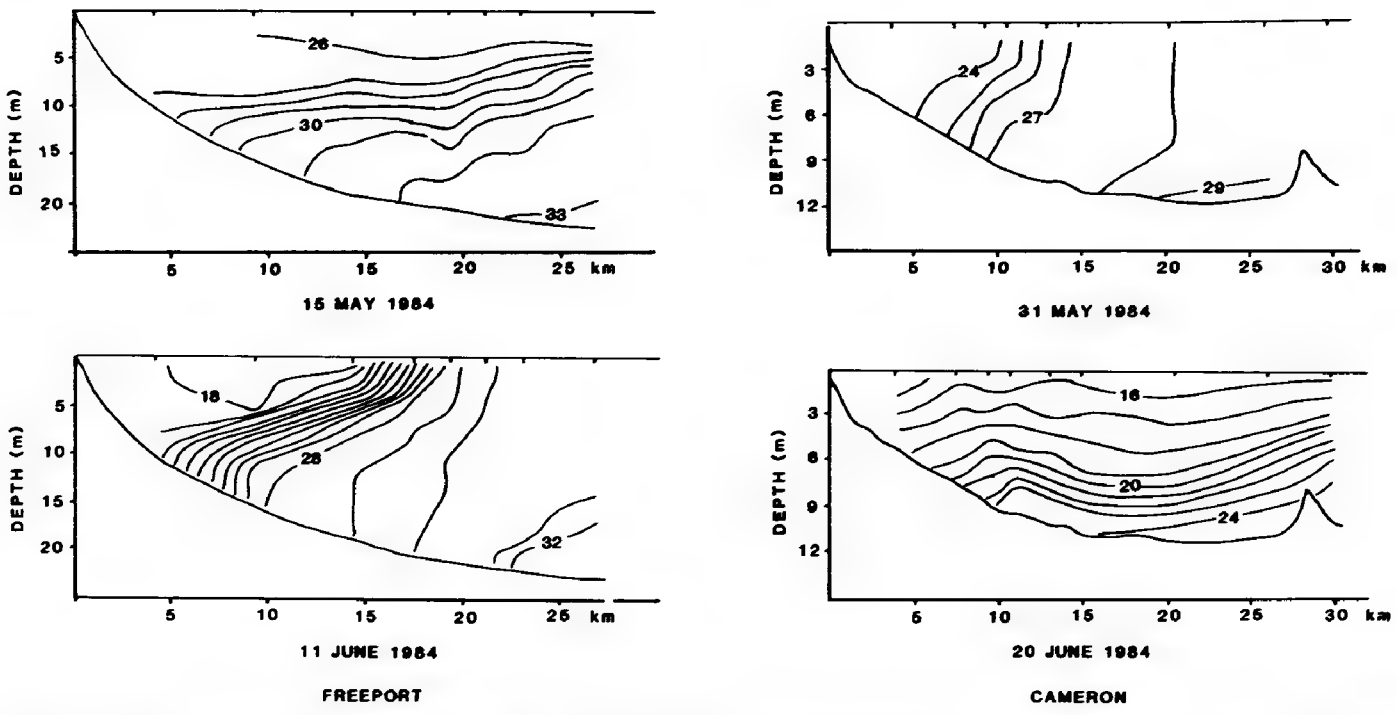


FIG. 6. Cross shelf salintiy profiles, Cameron, Louisiana and Freeport, Texas, in May and June 1984 (from Kelly *et al.* 1985a,b).

(*Micropogonias undulatus*), which is the most abundant species discarded on the white shrimp grounds off Texas (Chittenden and McEachran 1976). In addition, the possibility that commercial menhaden fishermen could have lost a net catch and caused the June or July kill has been discounted because TPWD reports indicate fish kills caused by menhaden fishing activity are numerically composed of 99% gulf menhaden. Our surveys found no menhaden vessels fishing off Texas and relatively few dead menhaden. These observations support our conclusion that commercial fishing activity was not primarily responsible for the June kill but was probably the source of the dead fish observed in July.

We suggest the sequence of events which produced the June 1984 phytoplankton involved Mississippi-Atchafalaya runoff which reduced salinities and transported nutrients into the Gulf, supporting a large phytoplankton bloom. The low salinity water and its associated bloom were concentrated near the Louisiana shore by winds, and then driven alongshore into Texas as a "jet" by the strong alongshore wind component in May. Oxygen consumption at night by phytoplankters, and by decay processes as the phytoplankton cells died and settled to the bottom, created an oxygen deficit which was intensified by stratification of the water column during calm weather conditions. These conditions ultimately resulted in the production of hydrogen sulfide which may have been responsible for most mortalities.

Because of the potential impact on coastal fisheries, further studies of the causes and effects of hypoxia are essential. Low D.O., however, is not always associated with mortalities; hypoxic D.O. values were reported off Freeport, Texas, coincident with reduced benthic abundances, but research divers found no evidence of widespread mortalities (Harper, McKinney and Nance 1984). We believe that the generation of hydrogen sulfide may be more

important in causing mass mortalities than low D.O. *per se*, and recommend that studies on the fate and effect of hypoxia routinely include the measurement of hydrogen sulfide in bottom waters and sediments.

ACKNOWLEDGMENTS

The following individuals provided information and/or support for this study: Dr. Laurel Loeblich, Department of Marine Biology, Texas A&M University at Galveston, identified dinoflagellates collected in the field and attempted to culture them; Dr. Thomas Minello, National Marine Fisheries Service, Galveston, provided salinity data; Dr. Roy Hann, Department of Civil Engineering, Texas A&M University, provided funds for the 19 June aerial survey; Mr. Frank Kelly gave permission to use figures from unpublished reports; Dr. David V. Aldrich, Department of Marine Biology, Texas A&M University at Galveston, reviewed the manuscript. This research was supported in part by Department of Energy contract DE-AC96-83P010850 to Texas A&M University through the Texas A&M Research Foundation.

LITERATURE CITED

BOESCH, D.F. (ed). 1985. Oxygen depletion on the inner continental shelf of the northern Gulf of Mexico: distribution, causes and effects. A strategy for monitoring and research. Louisiana Universities Marine Consortium, Chauvin, Louisiana. 12 pp.

BRONGERSMA-SANDERS, M. 1957. Mass mortality in the sea. pp. 941-960. In J.W. Hedgpeth (ed) *Treatise on Marine Ecology and Paleoecology*, Vol. 1. Ecology. Geological Society of America Memoir 67.

BRYAN, C.E., T.J. CODY and G.C. MATLOCK. 1982. Organisms captured by the commercial fishing fleet on the Texas brown shrimp (*Penaeus aztecus*) grounds. Texas Parks and Wildlife Department Technical Series. No. 31.

CHITTENDEN, M. and J. McEACHRAN. 1976. Composition, ecology, and dynamics of demersal fish communities on the continental shelf, with a similar synopsis for the entire Gulf. Texas A&M University Sea Grant Publication TAMU-SG-76-208. 104 pp.

COCHRANE, J.D. and F.J. KELLY. 1986. Low frequency circulation on the Texas-Louisiana continental shelf. *Journal of Geophysical Research*. 91(C9):10645-10659.

EPPLEY, R.W. and G.W. HARRISON. 1975. Physiological ecology of *Gonyaulax polyedra* a red water dinoflagellate of southern California. pp. 11-22. In V.R. LoCicero (ed) *Proceedings of the First International Conference on Toxic Dinoflagellate Blooms*. Massachusetts Science and Technology Foundation, Wakefield, Massachusetts.

ESAIS, W.E. and H.C. CURL. 1972. Effect of dinoflagellate bioluminescence on copepod ingestion rates. *Limnology and Oceanography*. 17:901-906.

FALKOWSKI, P.G., T.S. HOPKINS, and J.J. WALSH. 1980. An analysis of factors affecting oxygen depletion in the New York Bight. *Journal of Marine Research*. 38:479-506.

FIEDLER, P.C. 1982. Zooplankton avoidance and reduced grazing responses to *Gymnodinium splendens* (Dinophyceae). *Limnology and Oceanography*. 27:961-965.

FORSTER, G.R. 1979. Mortality of the bottom fauna and fish in St. Austell Bay and neighbouring areas. *Journal of the Marine Biological Association of the United Kingdom*. 59:517-520.

GARLO, E.V., C.B. MILSTEIN and A.E. JAHN. 1979. Impact of hypoxic conditions in the vicinity of Little Egg Inlet, New Jersey in summer 1976. *Estuarine and Coastal Marine Science*. 8:421-432.

GASTON, G.R. 1985. Effects of hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. *Estuarine, Coastal and Shelf Science*. 20:603-613.

———, P.A. RUTLEDGE and M.L. WALTHER. 1985. The effects of hypoxia and brine on recolonization by macrobenthos off Cameron, Louisiana (USA). *Contributions in Marine Science*. 28:79-93.

GRIFFITHS, A.B., R. DENNIS, and G.W. POTTS. 1979. Mortality associated with a phytoplankton bloom in Mounts Bay. *Journal of the Marine Biological Association of the United Kingdom.* 59:520-521.

GUNTER, G. 1979. Notes on sea beach ecology, food sources on sandy beaches and localized diatom bloom bordering Gulf beaches. *Gulf Research Reports.* 6:305-307.

HARPER, D.E., Jr., L.D. McKINNEY and J.M. NANCE. 1984. Benthos. Chapter 5. (92 pp.) In R. W. Hann and R. E. Randall (eds.) Offshore Oceanographic and Environmental Monitoring for the Strategic Petroleum Reserve. Annual Report for the Bryan Mound Site from September 1982 through August 1983. Department of Energy. Available from NTIS, Springfield, VA. DOE/P010850-2.

————, ————, R.R. SALZER and R.J. CASE. 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. *Contributions in Marine Science.* 24:53-79.

JOYCE, E.A., Jr. (ed). 1975. Proceedings of the Florida Red Tide Conference. Florida Marine Reserch Publication No. 8.18 pp.

JØRGENSEN, B.B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos.* 34:68-76.

KELLY, F.J., J.E. SCHMITZ, W.F. ULM, R.E. RANDALL and J.D. COCHRANE. 1985a. Physical oceanography. Chapter 1. (116 pp.) In R.W. Hann, C.P. Giammona and R.E. Randall (eds.) Offshore Oceanographic and Environmental Monitoring Services for the Strategic Petroleum Reserve. Annual Report for the Bryan Mound Site from September 1983 through August 1984. Department of Energy. Available from NTIS, Springfield, Virginia DOE/P010850-4.

————, ————, ————, ———— and ————. 1985b. Physical oceanography. Chapter 1. (92 pp.) In R.W. Hann, C.P. Giammona and R.E. Randall (eds.) Offshore Oceanographic and Environmental Monitoring for the Strategic Petroleum Reserve. Annual Report for the West Hackberry Site from November 1983 through November 1984. Department of Energy. Available from NTIS, Springfield, Virginia DOE/P010850-5.

KNUDSEN, K. and C.E. BELAIRE. 1975. Causes and probable correctives for oxygen depletion fish kills in the Dickinson Bayou estuary: a field study and simplified algal assay. *Contributions in Marine Science.* 19:37-48.

LoCICERO, V.R. (ed.) 1975. *Proceedings of the First International Conference on Toxic Dinoflagellate Blooms.* Massachusetts Science and Technology Foundation, Wakefield, Massachusetts. 541 pp.

OFFICER, C.B., R.B. BIGGS, J.L. TAFT, L.E. CRONIN, M.A. TYLER and W.R. JOHNSON. 1984. Chesapeake Bay anoxia: origin, development and significance. *Science.* 233:22-27.

PAFFENHOFER, G.-A. 1970. Cultivation of *Calanus helgolandicus* under controlled condition. *Helgolander wissenschaftliche Meeresuntersuchung.* 20:346-359.

PAVELLA, J.S., J.L. ROSS and M.E. CHITTENDEN, Jr. 1983. Sharp reductions in abundance of fishes and benthic macroinvertebrates in the Gulf of Mexico off Texas associated with hypoxia. *Northeast Gulf Science.* 6(2):167-173.

POKRYFKI, L.G. and R.E. RANDALL. 1987. Nearshore hypoxia in the bottom water of the northwest Gulf of Mexico from 1981 to 1984. *Marine Environmental Research.* 22: 75-90.

POLLUTION COMMITTEE, SOUTHERN DIVISION, AMERICAN FISHERIES SOCIETY. 1982. *Fish-kill.* 13:27-42.

RABALAIS, N.N., M.J. DAGG and D.F. BOESCH. 1985. Nationwide review of oxygen depletion and eutrophication in estuarine and coastal waters: Gulf of Mexico (Alabama, Mississippi, Louisiana and Texas). Final report submitted by Louisiana Universities Marine Consortium to Office of Ocean Assessments Division, NOS, NOAA. 60 pp.

ROUNSEFELL, G.A. and W.R. NELSON. 1966. Red-tide research summarized to 1964 including an annotated bibliography. U.S. Fish and Wildlife Service. *Special Scienctific Report-Fisheries.* No. 55. 85 pp.

SELIGER, H.H., J.A. BOGGS and W.H. BIGGLEY. 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. *Science.* 228:70-72.

SWANSON, L.R. and C.J. SINDERMANN. (eds.) 1979. *Oxygen depletion and associated benthic mortalities in New York Bight, 1976.* NOAA Professional Paper 11. 345 pp.

TAYLOR, D. and H. SELIGER (eds). 1979. *Proceedings of the Second International Conference on Toxic Dinflagellate Blooms*. Elsevier, Holland.

TAYLOR, F.J., N.J. TAYLOR and R.J. WALSBY. 1985. A bloom of the planktonic diatom, *Cerataulina pelagica*, off the coast of northeastern New Zealand in 1983, and its contribution to an associated mortality of fish and benthic fauna. *Internationale Revue der gesamten Hydrobiologie*. **70**:773-795.

TEMPLE, R.F., D.L. HARRINGTON and J.A. MARTIN. 1977. Monthly temperature and salinity measurements of continental shelf waters of the northwestern Gulf of Mexico. *NOAA Technical Report*. **SSRF-207**.

TREBATOWSKI, B. 1988. Observations on the 1986/1987 Texas red tide (*Ptychodiscus brevis*). Texas Water Commission Report 88-02. 48 pp.

WARDLE, W.J., S.M. RAY and A.S. ALDRICH. 1975. Mortality of marine organisms associated with offshore summer blooms of the toxic dinoflagellate *Gonyaulax monilata* Howell at Galveston, Texas. pp. 257-263. In V.R. LoCicero (ed.) *Proceedings of the First International Conference on Toxic Dinoflagellate Blooms*. Wakefield, Massachusetts.

WILSON, W.B. and S.M. RAY. 1956. The occurrence of *Gymnodinium brevis* in the western Gulf of Mexico. *Ecology*. **37**:388.